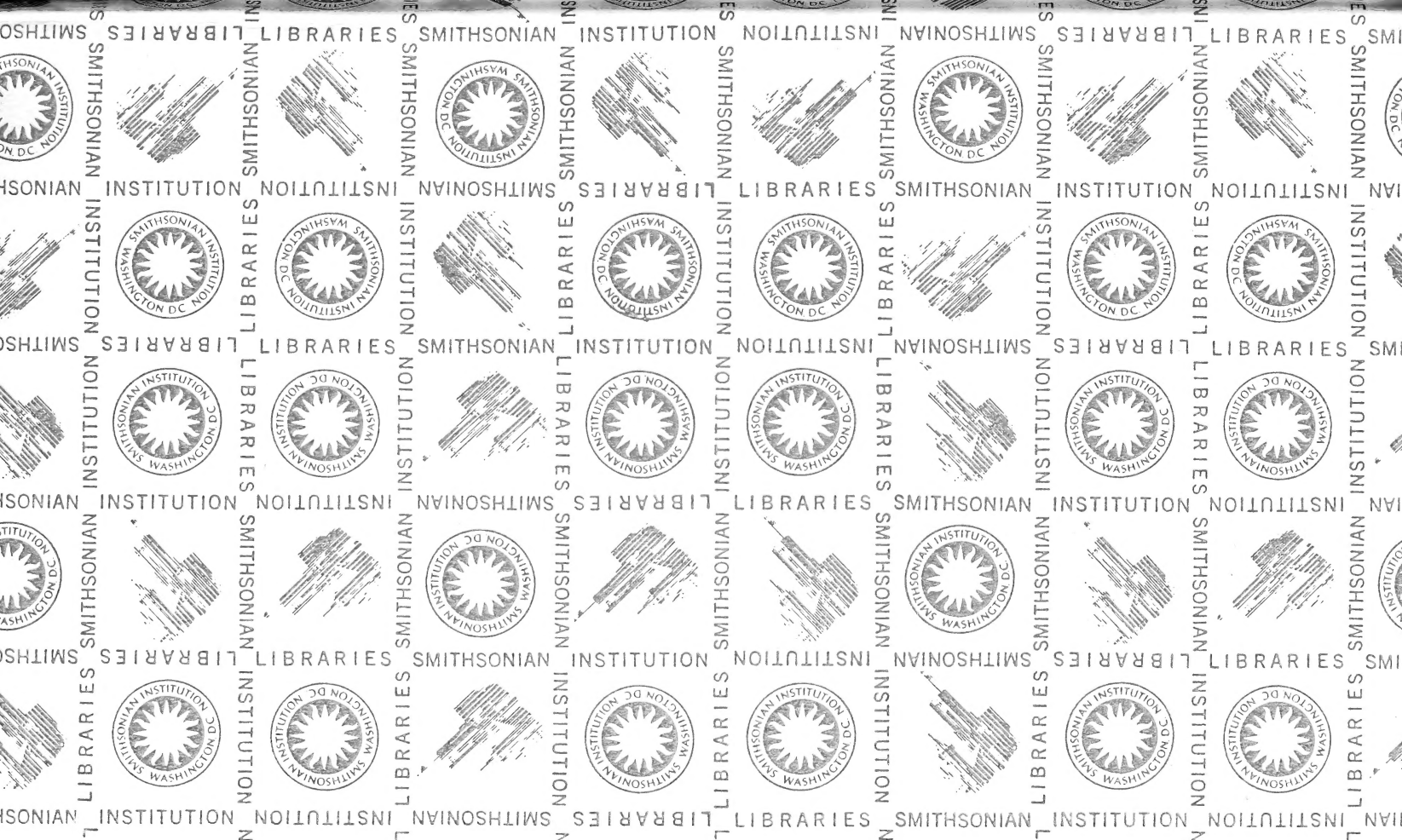
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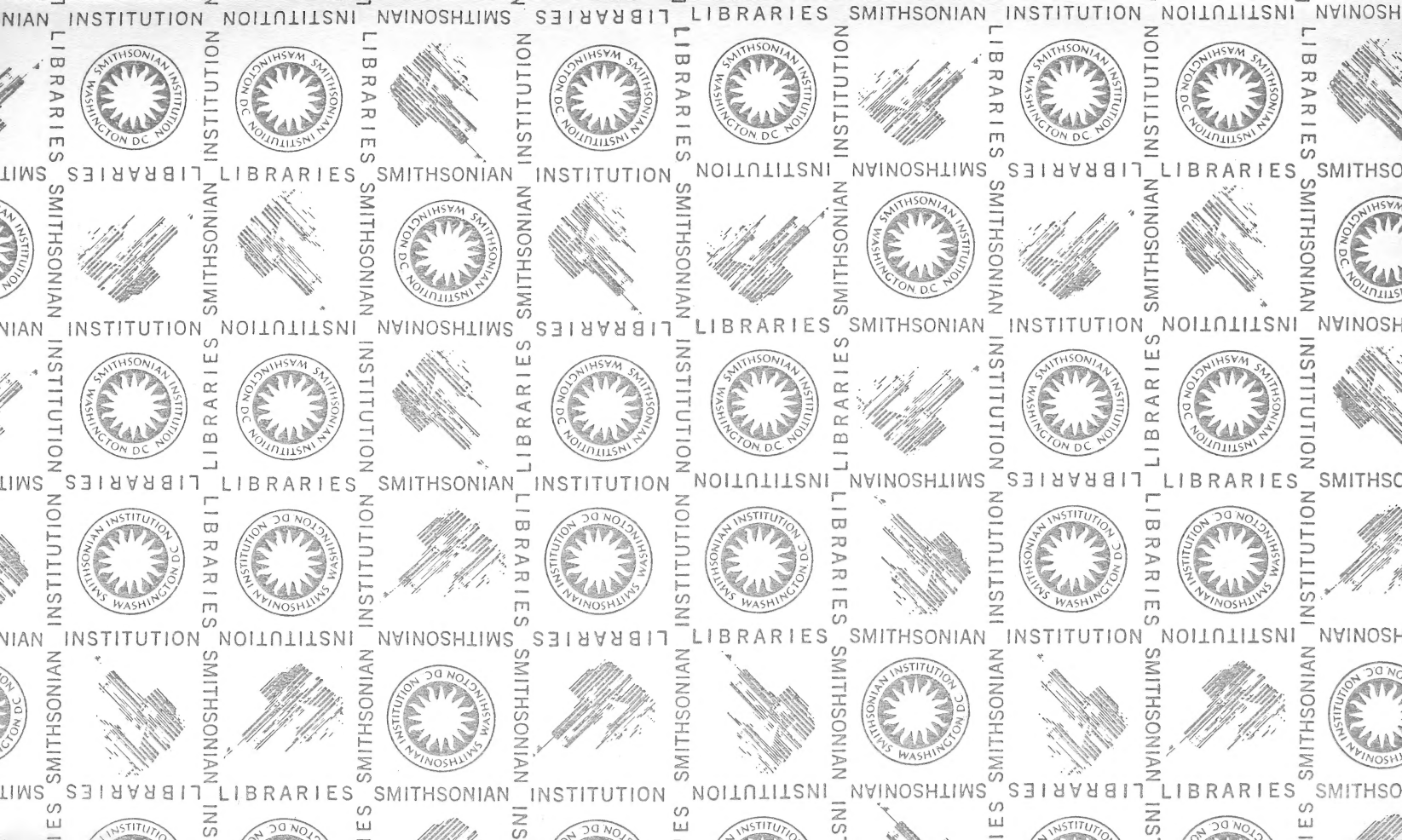
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PSYCHE

A Journal of Entomology

Volume 81

1974

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PSYCHE

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Vol. 81 MARCH, 1974 No. 1

CENTENNIAL ISSUE

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PSYCHE

Vol. 81 MARCH, 1974 No. 1

CENTENNIAL ISSUE

The Cambridge Entomological Club, the second oldest of the entomological societies existing in the United States, was founded on January 8, 1874. A few months later, on May 8, the first issue of its journal, *Psyche,* was published. In recognition of this anniversary, the Editorial Board of *Psyche* has designated this number of the journal, March, 1974, as the Centennial Issue. The leading article is a history of the Club, prepared by Janice R. Matthews and based on her careful study of the historical documents in the Club's archives. The members of the Cambridge Entomological Club are indebted to Mrs. Matthews for making her manuscript available to the editorial board and for her permission to publish it in *Psyche.*

The other articles in this issue are not directly related to the Centennial but it is worthy of note that all of them are authored, at least jointly, by members of the Cambridge Entomological Club.

We are indebted to Ward's Natural Science Establishment, Rochester, New York, for a helpful contribution towards the cost of printing this issue of Psyche.

— FRANK M. CARPENTER, *editor.*

PSYCHE.

ORGAN OF THE CAMBRIDGE ENTOMOLOGICAL CLUB.

EDITED BY B. PICKMAN MANN.

Vol. I.] Cambridge, Mass., May, 1874. [No. 1.

Introductory.

THE CAMBRIDGE ENTOMOLOGICAL CLUB was formed January 9, 1874, by the following persons, who met at Dr. Hagen's house, No. 7 Putnam Street, Cambridge, Massachusetts, namely: Messrs. E. P. Austin, Edward Burgess, G. R. Crotch, of Cambridge, England, George Dimmock, J. H. Emerton, Dr. H. A. Hagen, Messrs. Samuel Henshaw, B. P. Mann, H. K. Morrison, J. C. Munro, of Lexington; Dr. A. S. Packard, of Salem, Messrs. Eugene Schwarz, and S. H. Scudder. It has since added to its number Messrs. J. A. Allen, Walter Faxon, A. W. Gould, Prof. C. E. Hamlin, Messrs. Holmes Hinkley, H. G. Hubbard, Baron C. R. Osten Sacken, Messrs. F. G. Sanborn, G. D. Smith, P. S. Sprague, Roland Thaxter, of Newtonville, and C. P. Whitney, of Milford, N. H.

At the fourth monthly meeting, held April 10, 1874, the Club decided to undertake the publication of a monthly organ, to be called PSYCHÉ. This organ will contain such parts of the proceedings of the Club as seem to be of general interest, biological contributions upon Arthropoda from any competent person, lists of captures, with time and locality, miscellaneous entomological information, and especially a BIBLIOGRAPHICAL RECORD, in which last a list will be given of all writings upon Entomology published in North America, and of all foreign writings upon North American Entomology, from the beginning of the year 1874, with a brief note of the contents of each. For the greater perfection of this list, authors and societies are requested to forward their works to the editor at the earliest date possible.

Each number will contain at least four pages, and as soon as the returns are sufficient to make it possible, a greater number of pages will be given. The subscription price in

---

FRONTISPIECE: Facsimile of page one of the first issue of *Psyche*, May, 1874.

HISTORY OF THE CAMBRIDGE ENTOMOLOGICAL CLUB*

By Janice R. Matthews
Department of Entomology
University of Georgia
Athens, Ga. 30601

The Beginnings of the Cambridge Entomological Club

On a Friday evening, January 9, 1874, Dr. Hermann A. Hagen, Professor of Entomology at Harvard College and Curator at the Museum of Comparative Zoology, invited a group of twelve men to his home at 7 Putnam Street in Cambridge, to consider the question of forming an entomological society. Most of them had been meeting informally for several years as a section of the Boston Society of Natural History, but some had more ambitious plans. Wanting to publish a journal, to meet outside of Boston, and to have members from all over the country, they desired to form "an organization independent of any other" — which was to be the Cambridge Entomological Club.

Among the twelve present, probably the two most influential that first evening were Dr. Hagen and Samuel Scudder [1,2]. Dr. Hagen was the first professor of entomology in the United States; he had left Germany in 1867 at the invitation of Louis Agassiz to take charge of the entomological department of the Museum of Comparative Zoology in Cambridge, and had been appointed to his professorship at Harvard in 1870, at the age of 53.† But although

*This article is based on a term paper submitted in partial fulfillment of the requirements for the degree of Master in Arts in Teaching from Harvard University, 1967. The secretaries' records, minutes of the Club meetings, and other pertinent documents were placed at my disposal by the officers of the Club. In the present account, quoted passages without specific references are taken directly from the minutes of the meetings.

The original manuscript has been placed on permanent file with other Cambridge Entomological Club historical documents in the Museum of Comparative Zoology; it was revised and updated for publication here by the editor, F. M. Carpenter.

†Entomology had been recognized in America as a serious branch of science since the latter part of the eighteenth century, however. William Dandridge Peck [3], the first native born American entomologist, initiated the scientific study of insects at Harvard as that institution's first professor of natural history; as early as 1837 his student, Thaddeus W. Harris, while acting as librarian of Harvard College, gave a course in entomology that included brief field excursions [3,4]. Following Hagen's arrival in Cambridge, Harvard became a center of entomological activity, involving undergraduate and graduate students as well as more mature investigators.

Dr. Hagen had held his professorial position for four years now, his first course of lectures had been given only the previous summer, and its enrollment had been but one student, J. H. Comstock; when he did formally teach, Dr. Hagen's courses consisted of "lectures, given at rare intervals to advanced students." As this might indicate, Dr. Hagen's principal work and real devotion were centered about the Museum of Comparative Zoology, and to him other interests were secondary. So although most influential in the formation of the Entomological Club, and an enthusiastic supporter of its activities, Dr. Hagen did not wish any responsibility toward running it. Thus, when at this first meeting Dr. Hagen declined to take the chair (as he declined, or resigned from every office for which he was ever proposed in the Club), Samuel Scudder was chosen as chairman.

A graduate of Williams College and Harvard's Lawrence Scientific School, Samuel Scudder had been an assistant to Agassiz, and at the time of the Club's founding was nearly 38 years old. Once considered "the greatest Orthopterist America has produced," he also worked on the diurnal Lepidoptera and, as the foremost American student of fossil insects in his time, served as paleontologist to the U.S. Geological Survey from 1886 to 1892 [2]. Scudder was also a competent editor and a bibliophile; he served as assistant librarian of Harvard College and librarian of the American Academy of Arts and Sciences. Yet despite these and many other time consuming activities and before illness finally forced his withdrawal from active participation in 1903, he held various formal offices in the Cambridge Entomological Club for a total of eighteen years.

Samuel Scudder having been appointed to the chair, the meeting moved on to the first order of business — the establishment of some guidelines for the new organization. Voting to keep it as informal as possible, "no more rules being made than are necessary," the members decided that the new Cambridge Entomological Club should have only one permanent officer, a secretary; to fill this position, they wisely chose 26 year old Benjamin Pickman Mann [5]. The son of Horace Mann, well known as a teacher and advocate of public schools, Benjamin had graduated from Harvard College only four years previously. He was a conscientious researcher, a specialist in entomological literature and bibliography, who for many years to come would not only keep careful record of all Club proceedings, but serve as treasurer, librarian, and editor of the Club's publication.

After Mann's appointment and the decision to hold the next meeting at Scudder's home, the Scientific Communications of the evening

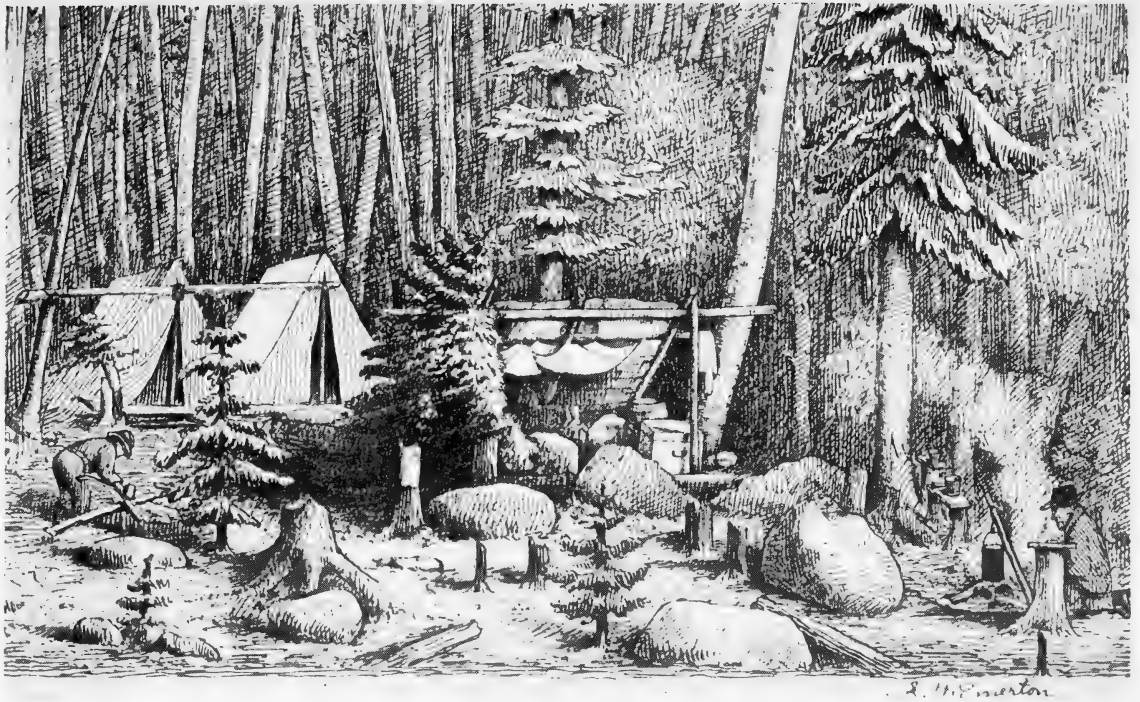
began. Dr. Hagen commented on the discovery of fossil galls, apparently caused by insects, preserved on a twig in amber from Maryland; this was of special interest to Hagen, since he had published extensively on Baltic amber insects while he was still in Germany. There then ensued a general discussion of "the senses by which insects are caused to assembly for sexual or other purposes." This must have been a particularly interesting discussion because of the varied backgrounds represented. For example, there was Dr. A. S. Packard, who had been one of Agassiz's students and who had just finished his third year as State Entomologist of Massachusetts [6]. He and Scudder were nearly the same age and they had been close friends since their undergraduate days, but Packard's experiences had been more varied: he had been a surgeon in the Civil War, a Custodian of the Boston Society of Natural History, a lecturer on entomology at Massachusetts Agricultural College and Bowdoin College; and he had studied marine life along the southeastern coast, and had published his well-known "Guide to the Study of Insects." However, his active association with the Entomological Club was to be very brief, for he was appointed to a professorship at Brown University in 1878, a position which he held until his death in 1905.

Then, in contrast, there was Edward Burgess, at the age of 26, a recent graduate of Harvard College and a former assistant in the Museum of Comparative Zoology; he was currently Instructor in Entomology at the College, giving the "course of elementary instruction in the study of insects." Although he became known in entomological circles for his published accounts of insect morphology, Burgess later won renown for his contributions to naval architecture [7]. At about the same age, there was James H. Emerton, who had already foretold his life interest by collecting spiders at over a hundred localities in New England [8]. A skilled artist, he had recently finished the first of innumerable illustrations he would make for A. S. Packard, S. H. Scudder, and many other zoologists. A trip to Europe and a position as curator in the museum of the Peabody Academy of Science at Salem soon removed him from the Cambridge scene for a few years but he continued to publish extensively on spiders and to take an active part in the Entomological Club until his death in 1931. Another member was Samuel Henshaw; at the age of 22 and without college training, he was at the time beginning to work on the insect collection at the Boston Society of Natural History; he subsequently became an assistant in entomology at the Museum of Comparative Zoology and later (1912-1927) its director

[9]. Of nearly identical age was George Dimmock, a Harvard freshman who had a strong interest in insects, especially Coleoptera and Lepidoptera. Although on graduating from college he spent several years at the University of Leipzig in Germany, from which he received his doctorate, he later returned to Cambridge and for many years continued to be active in the Entomological Club [10]. Youngest of all the founders of the Club was Herbert K. Morrison, only 19 years old, an energetic and serious student of noctuid moths. His experience on the first of the Club's excursions to the White Mountains in New Hampshire, a few months later, induced him to become a professional insect collector. During the next decade, he collected extensively in the United States, especially in such little-known regions as Washington Territory, Arizona, New Mexico and Nevada, and he furnished countless specimens of many orders to specialists in this country and Europe. His death at the early age of 31 terminated a brilliant entomological career [11].

Also at this first meeting there was a European coleopterist, Eugene A. Schwarz. Born in Germany, he received his training at the Universities of Breslau and Leipzig. In 1872, at the age of 28, he came to the Museum of Comparative Zoology as an assistant to Hagen. He was to stay in Cambridge only a few years, however, leaving in 1875 on several collecting trips and finally joining other entomologists in the U.S. Department of Agriculture in Washington, where he remained until his death in 1928 [12]. Very little can be said about the two remaining members present at the meeting. E. P. Austin, who was in the mining business, was an amateur coleopterist and published several papers on beetles in the course of the next few years, but he was not active in the Club after 1882. Even less is known of J. C. Munro, who lived in Lexington; he appears not to have attended any other meetings of the Club.

One individual, George R. Crotch, although not present at the first meeting, or in fact any other meeting of the Club, was regarded by all as one of the founders. He had become interested in insects, especially Coleoptera, while an undergraduate at Cambridge University in England. He had collected extensively in Europe and in late 1872 he had come to this country to collect insects in the western states. He was a very energetic and enthusiastic entomologist and a prolific writer [13]. In late 1873, at the age of 31, he accepted a position as assistant at the Museum with Hagen. By the end of that



Camp of the Cambridge Entomological Club, Mt. Washington, New Hampshire, July, 1874. [From an original drawing by J. H. Emerton in the C.E.C. archives.]

year, however, he had developed tuberculosis and was unable to attend the first meeting of the Club. He died six months later.*

At the second meeting, held at Scudder's house (156 Brattle Street), there were discussions of such topics as the identity of a borer destroying an elm tree at Henry W. Longfellow's house (Hagen), of the metamorphosis of the Saturniidae (Morrison) and of the preparation of lepidopterous larvae for preservation (Hagen, Scudder, Morrison). Seven new members were elected: J. A. Allen, C. E. Hamlin, and C. R. Osten Sacken, all assistants at the Museum; Dr. Walter Faxon, curator at the Museum; H. G. Hubbard and Roland Thaxter, both Harvard undergraduates; and C. P. Whitney, of Milford, New Hampshire, the first non-resident member. Osten Sacken began collecting insects, especially Diptera, when he was a boy in Russia; he was on the staff of the Russian Legation in this country for 27 years but at the age of 45, in 1873, he resigned to become an assistant to Hagen. He was an active participant in the Entomological Club for the entire period during which he was working at the Museum, but after experiencing two winters in Cambridge he moved to Rhode Island (a choice "influenced by the temperate winter-climate"); and in 1877, his work on the Diptera of North America finished, he returned to Europe [14]. Hubbard became acquainted with E. A. Schwarz at the meetings of the Club and shortly after they formed a collecting team, ultimately resulting in the famous "Hubbard and Schwarz" collection of Coleoptera [15]. The other undergraduate, Thaxter, started as an entomologist and was active in the Club for many years, his first ten papers being published in *Psyche*. However, his interest was directed by Professor Farlow towards fungi parasitic on insects, and he subsequently became Professor of Cryptogamic Botany at Harvard, with most of his research being on these parasitic fungi, especially the Laboulbeniales.

After the third meeting, the Cambridge Entomological Club gathered at a little building nicknamed the "entomologicon," situated in the backyard of B. P. Mann's residence at 19 Follen Street [16]. These early meetings had no planned program; at each meeting, a different member was chosen chairman and the minutes and acquisitions to the Club's library were read. The remainder of the meeting was then opened to general discussion and the exhibition of new

*The list of signatures of the founding members in the minutes of the first meeting includes a line that reads: "This was to have been the place for the name of George Robert Crotch, Cambridge, England."

New-England
JOURNAL OF EDUCATION.

Boston, Mass., August 21, 1875.

The Cambridge Entomological Club.

CAMP OF THE CAMBRIDGE ENTOMOLOGICAL CLUB,
MT. WASHINGTON, July, 1875.

MR. EDITOR:—This is the first uncomfortable day we have had. The clouds rise from the valley and descend from the summit by turns, driven by the shifting currents of air, and we get more of the fog and drizzly showers here on the middle of the mountain than they have either above or below us. Once in a while we catch a glimpse of Mt. Carter, with half a dozen little clouds playing a stately game of tag among his green ravines, or of the Glen House in the sunny valley, but it is only for an instant, and though we can hear the stage rattling along half a mile overhead, we have not seen the road above the trees since sunrise.

After passing the five-mile post an extensive view is opened toward Conway, taking in several very picturesque mountains and lakes, the summit of Mt. Washington tower on the right, and in the middle distance the rugged sides of the south wall of Tuckerman's ravine. Here is the beginning of the habitat of the Mountain Butterfly, a species peculiar to this locality and eagerly sought by nearly all our party. They have the curious habit of flattening their wings down upon the ground or rock when they alight to avoid the wind, but such is the force of habit that they do so when it is a calm also, raising them slowly afterwards as if it were a second thought. The caterpillars live on a coarse kind of sedge which grows here.

Proceeding to the summit we arrived in season to witness the ascent of the singular looking little engine and car. The engine being built for up-hill work seems, as one of the party aptly expressed it, to "tip down" as soon as it comes on the piece of level track in part of the platform. Most of us, after a rapid glance at three States and a hundred lakes and rivers, devoted our time to hunting Alpine beetles which abound under the rocks. Nearly all these are species peculiar to high mountains, but on fair days many butterflies, flies, and wasps wander up from the valleys. Returning by moonlight, we did ample justice to the fried hominy and syrup which the stay-at-homes had provided, and at ten o'clock when the rain came splashing down in torrents, most of us were too drowsy to think that the morrow's projected trip to Tuckerman's ravine must be abandoned.

Yours truly, WALTER HOXIE.

Portion of a letter written by Club member Walter Hoxie while at the C.E.C. camp, Mt. Washington, July, 1875, and published in the New-England Journal of Education. [Copy in C.E.C. archives.]

materials and curiosities. For its first three years, the Club continued in this strictly informal manner, and included not only regular meetings but excursions to areas of entomological interest.

At the 7th meeting, July, 1874, "the Chairman had to be contented with sitting on a rock instead of a chair, a feat which he performed with sufficient grace and dignity, wrapped in a blanket." This peculiar situation occurred because, during the summer of 1874, an "Entomologists' Camp" was held on Mt. Washington in New Hampshire, a "quarter of a mile below the Halfway House and far enough into the woods to be out of sight of the road." The party, including members and non-members alike, left Boston by Portland steamer, and remained in New Hampshire for almost a month; the expenses, including round-trip fare from Boston, were about twenty dollars apiece, and provisions, tents, etc., were provided by the Club Excursion Committee — Dimmock, Austin and Mann. A regular Club meeting was held, although it was "several times disturbed by Mr. Morrison's frantic attempts to capture the moths attracted by the sole luminary of the occasion, his own lantern." But in the main, these summer excursions were light-hearted affairs, and when the next Mt. Washington announcement, for July, 1875, stated that "members may invite the attendance of ladies," the ten men who appeared at the meeting had fourteen women with them.

In the early years, there was no intention to limit place of meetings, which were often held outside the borders of Massachusetts. Nor was there distinction made between resident and non-resident members. Both of these policies speedily changed the Club from a local organization to one including members from many parts of the country. By January, 1879, the secretary reported 47 members residing outside of New England, and only 19 within the area, most of them in the vicinity of Boston and Cambridge.

The Beginnings of Psyche

At the fourth meeting, on April 10, 1874, Samuel Scudder proposed that the Cambridge Entomological Club should begin publication of a monthly journal. A lively and lengthy discussion followed this proposal, ending in the decision to undertake such a project. The title of this new "Organ of the Cambridge Entomological Club," proposed by Scudder, was to be *Psyche,* derived from the Greek word for butterfly. B. P. Mann was elected as the editor for this new publication and "charged with the execution of all but the scientific

Camp of the Cambridge Entomological Club,

HALF-WAY HOUSE,

Mt. Washington, N. H.

All matters relating to tents, their location, etc. will be attended to by B. PICKMAN MANN, Camp Master, C. E. C.

NO SUGARING OF TREES ALLOWED WITHIN 500 FEET OF THE CAMP!!!

Memorabilia of the Mt. Washington camp of the Entomological Club, 1874 and 1875. Top: letterhead of camp stationery; middle and bottom: reproductions of signs posted at the camp.

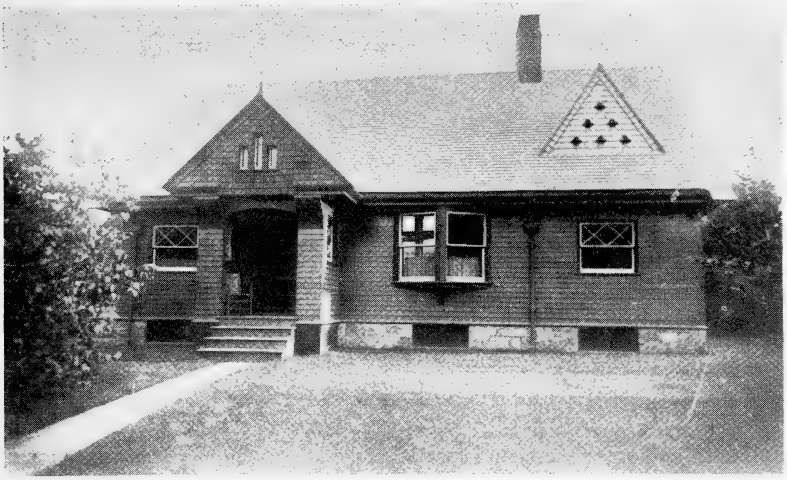
work, which latter the members were engaged to supply." The first number, to consist of four pages, was to be ready by the next monthly meeting of the Club, and the subscription price was set at one dollar per year. The Club thus began Volume 1 of *Psyche* (which, as completed, covers the years 1874-1876), as a place for publishing "biological contributions upon Arthropoda from any competent person," and miscellaneous entomological information, while assiduously avoiding "all discussion of vexed questions." However, economic entomology and taxonomic descriptions were less favored than contributions to general anatomy and biological entomology. But the most important part of *Psyche,* in the opinion of the founders, was to be the Bibliographic Record. Through this the Club set out ambitiously to record all writings upon entomology published in North America, and all foreign writings upon North American entomology, from the beginning of the year 1874, with a brief note on the contents of each. The original model for the Bibliographical

Record was clearly Hagen's *Bibliotheca entomologica,* which appeared in two volumes in 1862 and 1863.

The position of *Psyche* in the history of the Cambridge Entomological Club was to be a paradoxical one, for while it brought the Club into a position of national renown, at the same time it led to financial problems. Accordingly, early in 1876, the Club voted to establish annual dues of $2 for New England members and also designated a committee to raise a publication fund for *Psyche,* "the principal of the fund to be invested in trust securities" and the income to be used for the publications of the Club. A year later, January 12, 1877, there being no financial improvement and nothing in the publication fund, it was decided that additional measures should be "taken to increase the effectiveness of the work of the Club and to obtain money to defray the expenses of the Club and of the publication of *Psyche.*" Scudder's proposal, which was adopted, was that "an act of incorporation should be performed" and he advised the adoption by the Club of a Constitution and By-laws, "which must be in force as a preliminary to the act of incorporation." The Constitution and By-laws were promptly approved. At the following meeting, February 9, 1877, with a Justice of the Peace for Middlesex County in attendance, Scudder was elected President and Mann was elected Secretary and Treasurer, and these officers and the members of the executive committee signed the agreement of association. The Secretary of the Commonwealth, Henry B. Pierce, formally signed the Certificate of Incorporation on March 9, 1877.*

At the time of incorporation of the Club there were 48 members, half of the number being resident in the Boston-Cambridge area. The meetings were well attended, with an average of 11 members in addition to a few guests, and they were active affairs, having lively discussions. Most meetings were held at various members' residences, though some were held at an office that Scudder used for editing his journal, *Science.* Many additional non-resident entomologists were

*The Corporation was established according to the provisions of Chapter 375 of the Acts of the General Court of Massachusetts, passed in the same year as the founding of the Club, 1874. The incorporation apparently had no effect on the Club. No annual reports of the financial holdings of the Club were ever submitted to the Secretary of the Commonwealth, as required by law, and on March 24, 1964, eighty-seven years later, the Secretary of the Commonwealth dissolved the Corporation, in accordance with Chapter 180, section 26A, of the General Laws. Revival of the Corporation is, however, provided for in the legislative actions — *Editor*



Samuel Scudder's study in the yard of his house, 156 Brattle St., Cambridge. Consisting of a single large room, it included an extensive cabinet of insect drawers on one wall, a fireplace, and book shelves on two walls. The Cambridge Entomological Club held virtually all of its meetings here from 1888-1901. [Photograph, probably taken about 1890, in M.C.Z. archives.]

elected to membership, even some as officers of the Club, presumably as a means of increasing subscriptions to *Psyche*. One of the major interests of the members at this time, apart from *Psyche,* was the Club Library, the goal being to have in one place as nearly complete a collection of entomological publications as possible for the use of the members. This is not surprising, since both Scudder and Mann were bibliophiles. At first the secretary of the Club had the responsibility of recording all these accessions but in 1880 a librarian was elected. By 1886 the Club library included 1652 volumes and separates, which were at first housed in Mann's office but later transferred to Scudder's study.

The Lean Years

By 1890 the membership of the Club had changed greatly. Mann had left Cambridge permanently in 1887 to do bibliographic work for the Federal Department of Agriculture; and several other of the original members, including Austin, Dimmock, Morrison, Packard and Schwarz, had moved away from the Cambridge area, most

of them beyond New England. Financial problems at the Museum of Comparative Zoology, following Agassiz's death, reduced the funds available for assistants. Hagen, though he lived for another three years, was stricken with paralysis in 1890 and the February meeting of that year was the last he attended. During the period from 1890 to 1900, when the meetings were held in Scudder's study, only five resident members were elected to the Club, but four of these were to play a most important part in the history of the organization. One of them, A. P. Morse, then 28 years of age, was an assistant in the zoology department of Wellesley College; later he became associated with the Boston Society of Natural History, and still later with the Carnegie Institution of Washington, as a specialist in Orthoptera. He continued to be active in the Entomological Club for a total of 43 years, until his health failed in 1935 [17]. Another of the new members was F. C. Bowditch, an amateur coleopterist with special interests in the Chrysomelidae; in the course of his life he built up an extensive and important collection of the Chrysomelidae of the world, now at the Museum of Comparative Zoology [18]. The third of the members was J. W. Folsom, who was active in the Club while he was a graduate student at Harvard University. His early interests were in morphology and physiology of insects and he later taught entomology at the University of Illinois before becoming associated with the U.S. Bureau of Entomology [19]. The fourth of this group was W. L. W. Field, who joined the Club at the age of 19, while he was a first year student in Harvard College. He was an enthusiastic lepidopterist and published several papers in *Psyche* on inheritance in butterflies.* He attended meetings of the Club regularly and, as editor of *Psyche* from 1904-1909, was responsible for making significant improvements in its nature and content. Field did not continue in entomology, professionally, but taught biology at Milton Academy until 1917, when he became headmaster, a position that he held until 1942. These four members, in addition to Scudder, Henshaw and Roland Hayward (an amateur coleopterist who joined the Club in 1879 [20]), were the only individuals that attended the Club meetings

*At the Club's meeting in September, 1907, Professor William Bateson of Cambridge University, England, was scheduled to be the speaker; last minute changes prevented his coming, so W. L. W. Field "gave an interesting talk on the breeding experiments" that were being conducted by Bateson, who has "thus brought to the attention of the world again the long-neglected or forgotten Hereditary Laws discovered by Mendel."

from 1900 to 1903. The average attendance at these meetings, also held in Scudder's study, was between three and four.

The Harris Club

Just prior to 1900, another entomological club was formed, this time in the city of Boston. The moving force for this was Mr. H. H. Newcomb, an amateur lepidopterist and general insect collector. An organizational meeting was held on November 24, 1899, in his office on Court Street, Boston. The ten who were present were enthusiastic amateurs; most were in business or law, although a few were college students, not yet established professionally. W. L. W. Field, already a member of the Cambridge Club, was one of the ten and served as secretary of the new club for the three years of its existence. At their second meeting, the members decided on the name *Harris Club,* "in honor of Thaddeus William Harris, eminent among early American Entomologists, whose entire life was spent in the neighborhood of Boston."*

In many ways the Harris Club paralleled the earlier days of the Cambridge Club. From the beginning, the members agreed "that the organization should be as informal as possible." The constitution generally expressed the same goals as that of the Cambridge Club. And as did its counterpart, the Harris Club had a library, but of a much less formal and extensive nature. They were an extremely enthusiastic group and held several field excursions — only in their case to Mt. Katahdin in Maine. By 1903 the Harris Club included 41 local members, although the average attendance at the meetings for the previous year had been only 12. As Field noted in one of his annual reports, there had been a progressive decrease in the percentage of members attending as the total membership increased. Field undoubtedly provided a liaison with the Cambridge Club and was almost certainly responsible for the suggestion that the Harris Club merge with the older organization. On January 13, 1903, Field and Newcomb proposed:

> "That the Harris Club be merged in the Cambridge Entomological Club, all members of the Harris Club of record January 13, 1903, to be nominated on one ballot for membership in the Cambridge Entomological Club. The latter is an incorporated Club with a long and distinguished list of members, past and present.

*This was not the same organization as the Harris Entomological Club, which was founded in 1864 as a section of the Boston Society of Natural History and which was discontinued in 1886.

> It has a Publication Fund, and maintains a monthly journal, *Psyche*. It is believed by many local entomologists that one large club will be better than two small ones and that the members of the Harris Club will find many advantages in an alliance with the older organization. If the plan is carried out, the Cambridge Entomological Club will hereafter hold regular meetings in Boston."

This was unanimously voted by the Harris Club and at the February 13 meeting of the Cambridge Club the 38 active members of the Harris Club were nominated by Field and Hayward for membership. At the next meeting, March 13, all were elected, with only Field, Hayward and Bowditch (all amateurs) representing the Cambridge Entomological Club, Scudder being unable to take part because of his paralysis.

The change in the number and type of members rapidly led to a change in the nature of the Cambridge Entomological Club. The concept of a Club library very shortly came under critical examination, in part because of Scudder's illness and of the necessity of moving the library from his study. In three months the library committee, with Field as chairman, recommended that the Club library turn over whatever volumes the Boston Society of Natural History desired for its library, and to dispose of the rest among its members by auction. Thus, by a series of auctions presided over by H. H. Newcomb, most of the library was gradually disposed of at ridiculously low prices, until in 1909 the remaining works were sold for twenty dollars to a new member, W. M. Wheeler.

At the October meeting, 1903, the members considered the future of *Psyche,* which had been edited since 1891 by Samuel Henshaw.* A committee chaired by A. P. Morse, and including Bolster, Field, and Henshaw, was appointed to consider whether or not to continue its publication. In December, Field reported that "the committee was thoroughly in favor of maintaining *Psyche* as the journal of the Club and was ready to assume charge of the journal if that was the pleasure of the Club." It was and the editorship was assumed by W. L. W. Field; in November, 1906, the Club members discussed the Bibliographic Record, which had been the main part of the journal under Mann and Scudder, and decided to discontinue it and to devote the space to contributors' articles.

Other changes also began to manifest themselves. After 1903 the Club began to possess a very local outlook; the attempt to maintain a wide non-resident membership appears to have been abandoned. The attention of the Cambridge Entomological Club from 1904 to

CAMBRIDGE ENTOMOLOGICAL CLUB.

Regular meeting of the Club Friday, 14 Dec. 1883, at 7.45 p. m.

Mrs. A. K. Dimmock will show a collection of insects from *Betula alba* (the white birch).

Mr. G. Dimmock will describe a new mode of making preparations to show the double nature of the wing-membrane of insects, and will show some microscopical preparations of other parts of insects.

The meeting will be held at the Secretary's house, 54 Sacramento street, Cambridge. [The Porters station horse cars of the Charles river road, or the North avenue or Arlington cars of the Cambridge road, pass Sacramento street.]

☞*Annual election of officers at the meeting of 11 Jan. 1884.*

GEORGE DIMMOCK, *Secretary.*

Notice of the Club meeting for December 14, 1883, to be held at Dimmock's house on Sacramento St., with information about horse car transportation.

1909 seemed to focus almost totally upon its biggest project, the annual exhibitions of insect collections held in the late fall at the Appalachian Mountain Club, 1050 Tremont Building, Boston, and open to the general public. Several times, the announced topics for regular meetings were totally ignored, the entire program being devoted to the arrangements of exhibits and informal conversation. Often, nearly every other member had a box of specimens with him, mainly Lepidoptera, and during this period, members regularly exhibited entomological curiosities at the meetings as well.**

The Bussey Institution

In 1907 another event occurred which had great significance for the Cambridge Entomological Club. As far back as 1871, a few years before the Club was founded, Harvard College had established the Bussey Institution, located in Boston, as a place for courses in "practical agriculture," and for some years after that time offered

*Henshaw not only edited these volumes with great care but he personally covered all deficits resulting from their publication. At the meeting of March 8, 1901, the Club elected Henshaw a Life-Member, "as a token of the Club's appreciation of his generosity."

**This is the origin of the tradition, still maintained, that notices of the meetings should include the statement: "Members are invited to bring specimens to the meeting for demonstration and discussion."

The Bussey Institution, Forest Hills (Boston). The Club meetings were held in the library of this building from 1910-1929. This was the editorial office of *Psyche* and the official address of the Club. [Photograph in the Archives of the Harvard College Library.]

entomological instruction to undergraduates. The program was not very successful, however, and in 1907 the Bussey Institution was reorganized for graduate study and research in biology, including entomology. In 1908 William Morton Wheeler, a distinguished zoologist and entomologist, then curator of invertebrate zoology at the American Museum of Natural History, was appointed Professor of Economic Entomology at the Bussey Institution [21]. On his arrival he was elected to the Club and personally welcomed by President C. W. Johnson.*

In the following year Charles T. Brues was added to the Bussey Staff as Instructor in Entomology; and in November the Club gained by his election another member who would have an immediate and lasting influence on its future [23]. At the very next meeting, President Bolster reported the resignation of Field as editor of *Psyche*. "Mr. Brues, being called upon by the chair, said he would try to arrange things so that he could take up the work," thus beginning his distinguished term as editor, which would span the next 37 years.

The membership of Wheeler, Brues, and their graduate students served to draw the Cambridge Entomological Club closer to the Bussey Institution, not only intellectually but physically as well. Meetings during the post-Harris Club period had been held at various addresses around Boston: in the council room at the Boston Society of Natural History; at Emerton's room, Clarendon Street; at the Appalachian Mountain Club, Tremont Building; and at Newcomb's office, Court Street. At the February meeting, 1910, newly elected president Wheeler reported that certain rooms at the Bussey were being remodeled and he expressed his hope that future meetings of the Club might be held there. The suggestion was enthusiastically accepted and the members voted to hold the next meeting at the Bussey Institution, in Boston. That was the place of meeting for the following 19 years.

At this time a task of primary importance facing the Club and especially the new editor, C. T. Brues, was that of putting *Psyche* on a satisfactory financial basis; despite change in format, expenses continued to exceed subscription income and the contributions from

*C. W. Johnson became a member of the Club in 1903, shortly after the election of the Harris Club members, when he arrived in Boston to be curator at the Boston Society of Natural History, as a specialist in Diptera. A genial personality, with youthful and vigorous enthusiasm, he was a true naturalist and helpful to all who consulted him. He was active in the Club until his death in 1932 [22].

members were never great enough to give the Club working capital to use. Early in 1916 Brues recommended that the length of the articles be normally limited to eight pages and that articles of greater length should be paid for by the authors, who would also be required to bear the cost of the engravings for their illustrations and to pay the cost price for their reprints. Although this was approved, for many years the financial status of *Psyche* continued to fluctuate, primarily because of the lamentable absence of any substantial endowment to fall back upon in critical periods. Deficits did occur, sometimes amounting to several hundreds of dollars, but various members, notably Wheeler, Brues, Johnson, and Thomas Barbour,* made sufficient personal contributions to balance the accounts. Nevertheless, this was clearly the turning point in the history of *Psyche;* never again did the journal pass through such a protracted period of financial struggle as between 1895 and 1915. The Club members had every reason to be pleased at the Annual Meeting of 1919 as they heard the report of the acting treasurer, A. C. Kinsey: "At the close of a year of increased cost of everything it would not have been surprising if a financial report for the Club had presented a deficit . . . . Contrary to this, however, the cash balance to date is $118.35. This improvement in conditions should be credited in part to the increased efforts in collecting money due, but in a larger part to the efforts of the editor of *Psyche.* An adoption of this report should include an expression of thanks to the editor for his careful management of the cost of publishing the magazine."

During the first decade (1908-1918) of meetings at the Bussey, the Club was very busy giving a cordial welcome to the many new members elected during the period — a total of 92. Many of these were graduate students at Harvard and they enlivened the programs with accounts of their research and especially of their collecting trips. Among these, for example, was W. M. Mann, who, as one of Wheeler's students, collected extensively during his graduate years, even in such remote regions as the East Indies and South America. He published occasionally on ants after leaving the Bussey but for

*Dr. Barbour was elected a member of the Club in November, 1909, along with Brues, while he was a graduate student at Harvard. A vertebrate zoologist, he was soon appointed curator of reptiles and amphibians in the Museum of Comparative Zoology, and later served as Director of the Museum (1927-1946). However, he continued his membership in the Club and was very generous in his contributions towards the cost of publishing *Psyche.*

most of his life he was Director of the National Zoological Park and had little time for entomological studies [24]. Another student, James W. Chapman, was also a myrmecologist; in 1916, after graduating from the Bussey, he joined the staff of Silliman University, on the Island of Negros, Philippines, where he and Mrs. Chapman remained until the Japanese occupation in World War II [25]. A few of the Harvard faculty joined the Club and were active throughout this period, notably Nathan Banks, Curator of Insects at the Museum of Comparative Zoology, and G. H. Parker, Professor of Zoology at Harvard and for many years chairman of that Department. During this time also the Club included among its members a substantial number of enthusiastic amateurs, who took an active and important part in the meetings. P. G. Bolster, a practicing attorney, was a very effective collector, mostly of Coleoptera; he was president of the Club twice during this period, in 1909 and 1913 [26].* Another amateur active at this time was L. W. Swett, a proprietor of a store in Lexington; he built up a very large and useful collection of geometrid moths, now housed in the Museum of Comparative Zoology, and he was president of the Club in 1911 [27]. One of the most active of all Club members at this time was C. A. Frost, a civil engineer in Framingham. He was almost "the last of the old-time general students of Coleoptera and was most helpful to other coleopterists" [28]; he published about eighty papers, many of them in *Psyche,* and at various times served the Club as secretary and treasurer, and twice as president.

Among the newest elements in the Club membership in this decade were eight of the entomologists employed at the Gypsy Moth Parasite Laboratory of the Federal Bureau of Entomology, in Melrose Highlands. Included was the head of the control program for the Gipsy moth, A. F. Burgess, president of the Club in 1916.

As might be expected, the meetings were well attended, with an average attendance of about twenty. The programs were varied but usually included a main speaker and two or three shorter presentations. The meeting of June 17, 1919, might well serve as an example of one of this period, as well as of the decade to follow. The main feature of the evening was an address by A. C. Kinsey, a graduate student, on the origin of some biological characteristics of gall wasps.

*In 1909 Bolster prepared a manuscript on the history of the Club, the substance of which was read to the members on his retirement from the presidency in 1909. This was never published but is included in the archives of the Club.

Cambridge Entomological Club

LECTURES ON INSECTS

These lectures will treat in a popular way of the habits, growth and structure of Insects and their adaptation to their surroundings. They will be abundantly illustrated by the stereopticon and by motion pictures as far as they can be obtained.

Saturday afternoons at 2:30, March 12 and 19, April 16 and 23.

The lectures will be by the following well-known members of the Club:

March 12. The Butterflies—by W. L. W. Field, Headmaster of Milton Academy.

March 19. The Dragonflies—by R. Heber Howe, Jr., Master of Natural Science at the Middlesex School.

April 16. Ants and the Social Life of Insects—by W. M. Wheeler, Professor of Entomology at Harvard University.

April 23. Plant Galls and the Insects that Produce them—by A. C. Kinsey, of Indiana University.

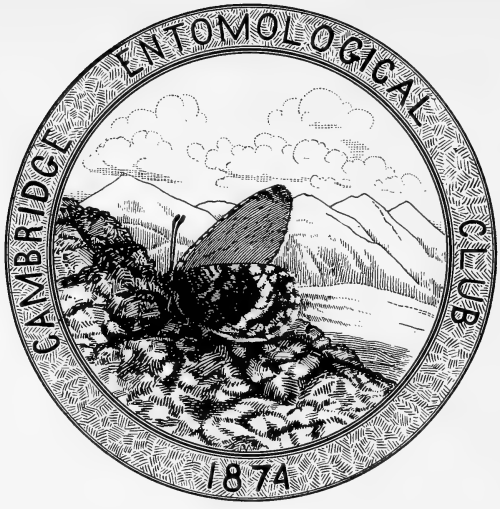
Tickets for the course, $2.00, for sale at the Bussey Institution, Forest Hills, Boston, Mass. Sent by mail on receipt of price. Make checks payable to Cambridge Entomological Club. Course and single tickets for sale at Tremont Temple on days of lectures.

Announcement of the public lectures given in Boston (1921) by members of the Cambridge Entomological Club.

Mr. Emerton followed, speaking of his recent spider-collecting trip to Cape Cod; Dr. Wheeler exhibited specimens of the Japanese beetle, recently introduced into New Jersey, and a drawing of a "peculiar, elongate ant" from South America. Mr. Frost gave a number of collecting notes on beetles and spoke of his success in rearing sumac borers from dead twigs. The meeting concluded with a discussion of insects as food by a visiting entomologist from Belgium, Dr. J. C. Bequaert, his account being based on experiences in the Congo region of Africa; and Dr. Wheeler remarked on his observations of similar foods used by the Australian natives.

One of the important projects of the Cambridge Entomological Club in the early twenties was a series of lectures given in Boston for the public at large. The first formal note of this idea was in October, 1920, when a committee of four was appointed to propose plans. In the course which these affairs often follow, three of the four ended up as lecturers as well — W. L. W. Field, R. H. Howe, and W. M. Wheeler; the fourth member of the committee, J. H. Emerton, having reached 72 years, preferred not to undertake a lecture, and A. C. Kinsey, then at Indiana University, was selected to take his place. All were to speak on their "well known specialities" at Tremont Temple, on four successive afternoons during the spring of 1921. The printed announcement of the lectures stated: "These lectures will treat in a popular way of the habits, growth and structure of Insects and their adaption to their surroundings. They will be abundantly illustrated by the stereopticon and by motion pictures as far as they can be obtained."

The lectures were quite a success, with an average attendance of about 150 persons, and income from ticket sales ($2 for the entire course, or fifty cents per lecture at the door) nearly equalled the expenses. Inspired by this, the Club voted the following year to expand the series to six lectures. Post card notices were sent to the Audubon Society's mailing list of 4,000 names, advertisements were placed in the *Boston Transcript,* and printed posters sent to libraries, schools and clubs. The lecturers included L. O. Howard, W. T. M. Forbes, J. C. Bradley, C. T. Brues, Miss Edith M. Patch, and even J. H. Emerton. However, the series of six lectures appears to have been too long, for only 41 course tickets were sold, more than half of each audience paying at the door, and attendance varied greatly from lecture to lecture. The average attendance was smaller than in 1921 as well, only between 50 and 100 persons. Because of its enthusiastic advertising campaign, the club went $230 in debt,



Seal of the Cambridge Entomological Club, designed by A. P. Morse and adopted by the Club in January, 1922. The White Mountain Butterfly (*Oeneis melissa semidea*) is shown resting on rock-fragments, with Mt. Washington and the rest of the presidential range (New Hampshire) in the background.

and, having no funds set aside for this, had to solicit for the deficit from its members. For this reason, the lecture series was discontinued and never revived.

At the very same meeting at which the Club made the decision to hold their first public lecture series, they also (upon the motion of Dr. Wheeler) appointed a committee to look for a design for a Club seal. Emerton, Wheeler, and Morse were appointed, and for the next two years they examined and exhibited at meetings the numerous designs submitted by members. Finally, at the Annual Meeting, January, 1922, the committee recommended a design by A. P. Morse, showing the White Mountain Butterfly (then known as *Oeneis semidea*), "perched characteristically on the dark grey, deeply weather-bitten rock-fragments of its mountain home, whose tints and texture its own so closely resemble, that when lying on its side with wings closed to escape the wind it becomes almost invisible. Beyond it at the right is suggested the sedgy slope of 'Semidea plateau' (so christened by Scudder) with its rock-rivulets in whose crannies the but-

terfly often seeks shelter from the furious blasts which sweep over the summits even in midsummer. Beyond, from the depths of the Great Gulf, rise the slopes of the northern peaks, Mts. Jefferson, Adams, and Madison, with Mt. Washington suggested at the left. Over all float the summer clouds which often shroud the summit of Washington for days at a time even when the other peaks are free" [29]. The seal was used on the cover of *Psyche* for the next 37 years, until 1959, and is reproduced on page 24 of the present issue.

During the second decade of the Bussey meetings 62 members were elected — less than in the previous period but a clear indication of the continuing vitality of the Club. Some of these new members were to have an active part in the future of the Club. For example, George C. Wheeler, one of W. M. Wheeler's students, was elected in 1920; still an active member of the Club, he is a frequent contributor to *Psyche*. F. M. Carpenter, a high school senior who had been attending some of the meetings since 1920 as a guest of F. W. Dodge, was elected in April, 1922; he became associate editor of *Psyche* eight years later and then editor after Brues' retirement in 1947. Dr. J. C. Bequaert, who had been a guest at several earlier meetings, was elected to membership in 1923, having been appointed in medical entomology in the Harvard Medical School; later, he succeeded Banks as Curator of Insects at the Museum of Comparative Zoology and participated in the Club meetings until his retirement in 1956. At the meeting of January 8, 1924, P. J. Darlington, Jr., an undergraduate in the College, was elected to membership; he also took an active part in the Club's affairs and followed Dr. Bequaert as Curator of Insects at the Museum. That particular meeting, incidentally, was the 50th anniversary of the founding of the Club, although the minutes refer to it only as the 50th annual meeting. J. H. Emerton, still regularly attending the meetings, gave a brief account of the history of the Club from 1874 to 1910 [30] and W. L. W. Field spoke about the Harris Club and read letters from two of the original members of the Cambridge Club — B. Pickman Mann and E. A. Schwarz.

Return to Cambridge

Towards the end of the twenties, plans were made by the Harvard Administration to terminate the Bussey Institution as a graduate school and to centralize biological instruction and research in a complex of buildings near the Museum of Comparative Zoology. The

new building, first named the Biological Institute but later termed the Biological Laboratories, was to be ready for occupancy in 1931. Impatient to become established in Cambridge, Professor Wheeler moved to temporary quarters in the Museum of Comparative Zoology in 1929, bringing with him the rest of the entomological staff and their graduate students. At the October meeting, 1929, the members of the Club voted to hold future meetings in Cambridge and left it to the executive commitee to find appropriate quarters for the gathering. Since the privilege of smoking was apparently a requirement, satisfactory housing was found in the basement of the Peabody Museum, adjoining the Museum of Comparative Zoology. Accordingly, on November 12, 1929, with President Carpenter in the chair, the Club met again in Cambridge. As the secretary of the Club, R. P. Dow, recorded in the minutes: "This was the first meeting of the Club in Cambridge since March, 1903, when the entire Harris Club was elected to membership." For the next two years the Club met in the Peabody Museum, in an exotic-looking room, decorated with examples of ancient Indian cultures, until the Biological Institute was completed. On October 13, 1931, the 498th meeting of the Club was held in room B-455 of the Biological Institute, with President C. A. Frost in the chair. Since that time, except for a short interval during World War II, the Club has met in that room, over a period of 43 years, and the formal address of the building, 16 Divinity Avenue, has been the official address of the Club.

Two months later, December, 1931, a most unusual meeting was held — the 500th meeting, which apparently holds the record for

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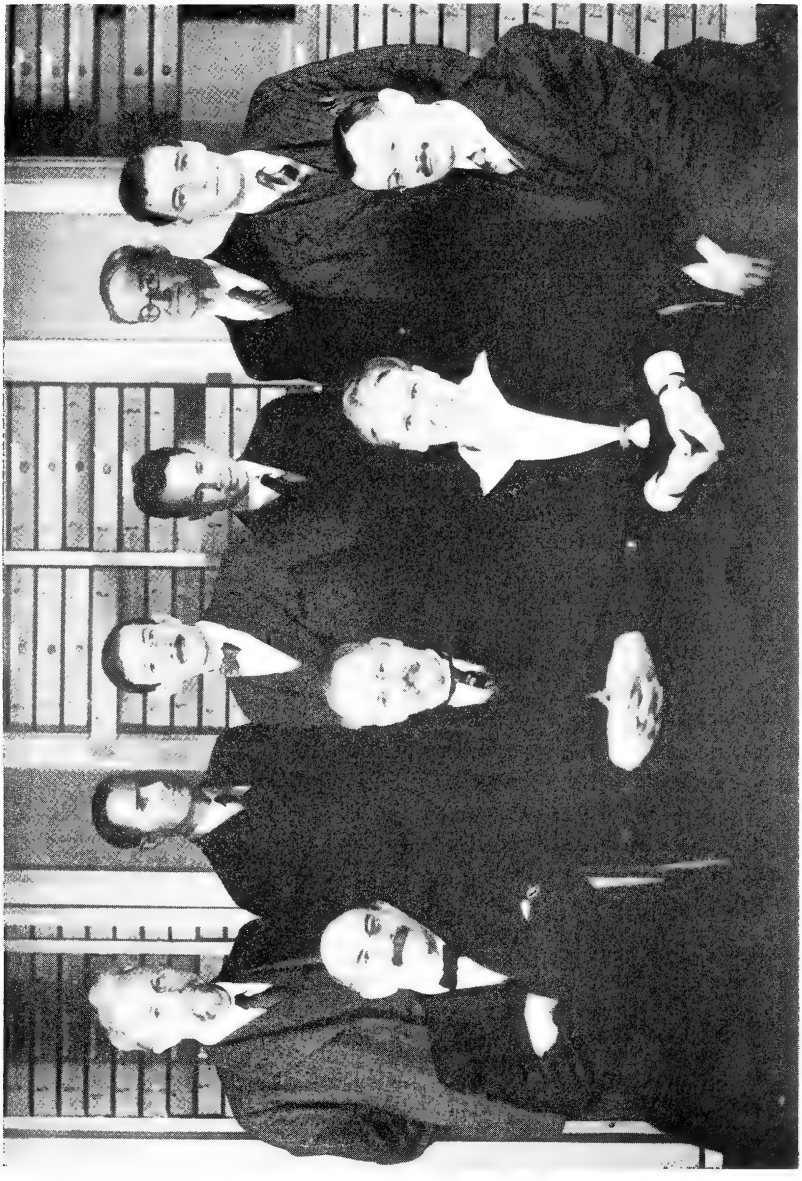
Explanation of Photograph on Opposite Page

Some members of the Cambridge Entomological Club in 1929. Front row (left to right), Charles W. Johnson, Curator at Boston Society of Natural History; Nathan Banks, Curator of Insects, Museum of Comparative Zoology; Elizabeth Bryant, Assistant Curator of Insects, M.C.Z.; J. C. Bequaert, then Associate Curator, later Curator of Insects, M.C.Z. Back row (left to right): Albert P. Morse, Curator of Natural History, at Peabody Museum, Salem; Arthur Loveridge, then Assistant Curator of Herpetology, M.C.Z., and collector of African insects; Charles T. Brues, Associate Curator of Insects, M.C.Z., and later Professor of Entomology at Harvard; E. T. Learned, Boston physician and lepidopterist; Samuel E. Cassino, Salem publisher (Naturalists' Directory), engraver, and lepidopterist; Frank M. Carpenter, then postdoctoral fellow at Harvard and president of the Cambridge Entomological Club. The photograph was taken in one of the entomological rooms in the M.C.Z. [Original in archives of Cambridge Entomological Club.]



Some members of the Cambridge Entomological Club, 1929. For explanation, see opposite page.

length and variety. In recognition of the occasion, a special program and dinner at the Faculty Club of Harvard University were held for the 29 members and one guest present. W. L. W. Field was toastmaster of the evening; he read the minutes from the first Club meeting in 1874, and a letter from Henshaw expressing regret at being unable to attend. The first after-dinner speaker was Nathan Banks, who "emphasized the need for specialization and the furtherance of systematic entomology." Next, C. W. Collins, of the Parasite Laboratory in Melrose Highlands, brought the felicitations of the Bureau of Entomology and traced the development of economic entomology during the Club's existence. C. T. Brues gave a humorous account of "some of the peculiar and amusing incidents" connected with his editorship of *Psyche*. C. W. Johnson and A. P. Morse spoke on the history of the Club (with no extant record of their remarks). Following these speeches, a motion picture on the life history of the yellow fever mosquito was shown. And then the regular scientific program of the evening began, a talk by Dr. Joseph Bequaert on "Some Problems of Medical Entomology in Guatemala." When the 500th meeting finally adjourned, it was 11:00 p.m.

Between 1920 and 1940, there occurred a striking transition in the composition of the Cambridge Entomological Club. Through the early twenties, the Club consisted of "not-all-terribly-old amateurs, more or less old professionals, and a few young people" [31]. But it was the custom in those days to pass the presidency and vice-presidency of the club around among the senior people, and so rotated that every few years the same man would be president again. In 1929, however, the tradition was broken by the election of Frank M. Carpenter, then a research fellow, to the presidency. His address as retiring president at the end of the year was published in the next issue of *Psyche* [32]. Dr. Carpenter was reelected as president for the following year, thus once again breaking tradition, for he was only the third person in the history of the Club to hold two successive terms of this office.* From this time the Club began to have an increasing number of younger members, including graduate students, as its officers.

*The others were Edward Burgess, 1879 and 1880; and J. H. Emerton, 1904 and 1905. In later years there were two other reelections: C. T. Brues, 1944 and 1945; and E. O. Wilson, 1954 and 1955.

World War II

During the thirties, the Club meetings were enthusiastically attended, the average being about 22. But this situation was shortly to change with entrance of the country into World War II. The December, 1941, meeting was held only two days after Pearl Harbor. No recorded mention of the war was made, however, until the following February, when a symposium on Insects and the War was held at the regular meeting. Discussions were presented by Dr. Bequaert of the Medical School, Dr. J. E. Gordon of the Harvard Medical Unit in England, Dr. A. Getty of the Massachusetts Bureau of Public Health, and Dr. C. B. Philip of the U. S. Public Health Service. These speakers considered the expected increase in insect-borne diseases among the public in general, as a result of the rapid transfer and movements of armed forces.

The Second World War had many more direct effects on the Club than the First did. By 1943, attendance at meetings was down to 7 or 8 members and it was apparent that the situation was going to become worse in the days immediately ahead, as one after another of the Club's members left to serve, directly or indirectly, in the war. In December, 1943, with only Carpenter, George Erickson (the Club's secretary), and one other member present, the meeting was held at the Harvard Faculty Club library, "where they discussed possible means whereby an active nucleus of the Club might be maintained during the War." For all of 1944 this small group of three or four met at the library on the second Tuesday of each month to carry on the Club's tradition. Some type of program was always included. At the meeting of February 15, for example, Private Floyd Werner (elected a member in 1939), on leave from the army, presented a paper on the "Distribution of Certain Species of the Beetle Genus *Epicauta*." In another year, the war was coming to a close and members began returning; and by the end of 1945 the meetings reverted to their pre-war time, place and vigor. The "active nucleus" had indeed been maintained, and the continuity of the Club insured.

Recent Years

Since 1950 the Club has continued with notable consistency, though with some obvious and distinctive trends. The attendance at meetings, for example, has been on the increase. The average attendance for the meetings of the decade 1953-54 to 1962-63 was 29, with the election of 62 new members; the average for the period from 1963-64 to 1972-73 was 38, with election of 133 new members. Although

many of the members elected were graduate students living in the vicinity of Cambridge, there has been a noticeable increase in the number of amateurs that have joined the Club and that have regularly attended the meetings. From 1903, when the Harris Club members were elected, through the Bussey meetings in the twenties, non-professionals made up about half of the membership in attendance. This may have been due in part to W. M. Wheeler's encouragement of amateur naturalists and his open expression of high regard for their contributions both to research and to the training of biologists.* However, during the thirties and forties, perhaps as a consequence of the depression and of World War II, the number of non-professional members in the Club dropped significantly. In the course of the past two decades, this trend has been reversed.

Other trends in the nature of the membership during the past two decades are apparent. For example, more women have joined the Club and taken part in the programs than previously. In the late fifties the Club experienced the greatest infusion of feminine talent in the entire history of its administration, with the election of Ruth Lippet Willey as secretary (1955) and Margaret C. Parson as secretary (1957), vice-president (1958) and, in 1950, as the first lady president of the Entomological Club.

Another striking change has been the increase in the number of arachnologists in the Club. The study of spiders was well represented in the Club from the very beginning by J. H. Emerton, one of the founders; as shown by the minutes of the meetings, he often spoke on habits of spiders — flying spiders were his favorite topic — and he published many papers in *Psyche*. After his death in 1932, spiders were almost never mentioned at the meetings until 1956, when Dr. Herbert Levi was appointed at the Museum of Comparative Zoology and became a member of the Club. He was promptly joined by a series of enthusiastic students of spiders (and even of millipedes). Such was their productivity that in 1964 Dr. Carpenter, while exhibiting the December issue of *Psyche,* felt compelled to note "what he interpreted as a hopeful trend in the fact that the number

*In his address, "The Dry-Rot of Our Academic Biology," at the Boston meeting of the American Society of Naturalists in 1922 Wheeler advocated the "utilization by the instructor of competent amateur naturalists as occasional assistants" and he continued: "We have all known amateurs who could make an enthusiastic naturalist out of an indifferent lad in the course of an afternoon's ramble, and, alas, professors who could destroy a dozen budding naturalists in the course of an hour's lecture." [33].

of pages devoted to insects was greater than the number devoted to spiders."

In March of 1965 the meeting commemorated the hundredth anniversary of Professor W. M. Wheeler's birth. Miss Adeline Wheeler, his daughter, attended the meeting and made available an exhibit of some of his original drawings. A complete set of his publications was also shown and several members discussed his contributions to the study of social insects. Three of the members present, Dr. F. M. Carpenter, Dr. E. O. Wilson and Robert W. Taylor (president of the Club), represented three successive generations of ant students that began with Professor Wheeler.

The story of *Psyche* since 1950 has been one of slow but steady growth with respect to both its size and the number of subscribers. With the retirement of Professor Brues as editor in 1947, the Club elected as the new editor Frank M. Carpenter, who had been associate editor of *Psyche* since 1928. The journal now has the largest number of subscribers in the Club's history; 115 of these are Club members, the rest being libraries or other institutions. The policy approved by the Club in 1916, i.e., requiring payment by authors for at least partial cost of printing of their articles, has prevented the occurrence of the deficits that plagued the journal in its earlier years. The more general acceptance of this policy by educational and other institutions, including the federal government, has allowed the publication in *Psyche* of more articles than would otherwise have been possible. In the past twenty years the average number of pages per volume has increased from 130 to 370.

The back issues of *Psyche,* now comprising 80 volumes, have created a storage problem. In 1930, when the editorial office moved to Cambridge, they were stored in the attic of the Museum of Comparative Zoology. In 1964 space needs of the Museum staff necessitated the removal of the volumes and on April 14, 1964, the Club voted approval of a contract for the storage of the back issues with the Johnson Reprint Corporation in New York, which also was authorized to serve as the Club's agent in selling the back issues. In 1972, however, as a result of a generally depressed economic situation, the Reprint Corporation asked that the contract be terminated and that the volumes be disposed of in some way. Fortunately, very satisfactory space for them was found in the basement of the Museum, along with its own publications, and early in 1973 the back volumes, weighing some 6,000 pounds, were returned to Cambridge and deposited in the Museum.

The Centennial of the Founding of the Club

At the May meeting, 1973, the Club voted that the officers for 1973-74 (including the elected members of the Executive Committee and the members of the Editorial Board of *Psyche*) constitute a Centennial Committee, with authority to make arrangements for appropriate recognition of the 100th anniversary of the Club. In October President Hölldobler reported for the Committee that the centennial celebration was planned for April 8 and 9, 1974. Professor Thomas Eisner of Cornell University, a member of the Club since 1950, would present a public lecture on the first day, on a topic of general interest. The entomological and arachnological sections of the Museum of Comparative Zoology and the Museum Laboratories would hold open-house on the afternoon of the second day, followed by a dinner and the Centennial Meeting at the Harvard Faculty Club. The March issue of *Psyche* was to be the Centennial Issue and would include an article on the history of the Club.

These plans were effectively carried out. Dr. Eisner's lecture, entitled *On Insects and How They Live as Chemists,* was given to a capacity audience in the main lecture room of the Biological Laboratories. At the open-house on Tuesday, the new entomological facilities and equipment in the Museum Laboratories were demonstrated by Professors Hölldobler, Wilson and Levi, and the insect collections at the Museum were shown by Dr. John Lawrence. Photographs and documents from the Club's archives were on display.

The dinner at the Faculty Club was attended by fifty members and guests; among the guests were Dr. Miriam Rothschild of England and Dr. Clark A. Elliott of the Harvard University Archives. Following the dinner, Professor F. M. Carpenter spoke on the subject, *Aspects of the History of the Cambridge Entomological Club — Somewhat Anecdotal.* He discussed the general status of entomology and related fields of biology when the Club was begun, with examples from the Club's records, and reviewed the achievements of the thirteen men who founded the Club. In the course of the past century about 800 individuals have been members of the society. With a current membership of slightly more than a hundred members, mostly local, the Club continues to be vigorous and active. *Psyche,* with an accumulated pagination of about 20,000 in its eighty volumes, now has some five hundred individuals and institutions on its subscription list. In his final remarks, Professor Carpenter em-

phasized the close association that has existed between the Cambridge Entomological Club and the Museum of Comparative Zoology, beginning with the founding of the society by Professor Hagen and his associates at the Museum. He stressed the need for continuing this relationship.

With this Centennial Meeting, the Club began its second century.

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OFFICERS OF THE CAMBRIDGE ENTOMOLOGICAL CLUB

Date of Election	President	Vice-President	Secretary	Treasurer
Jan. 1874			B.P. Mann	
Jan. 1875			B.P. Mann	
Jan. 1876			B.P. Mann	
Feb. 1877	S.H. Scudder		B.P. Mann	B.P. Mann
Jan. 1878	E.P. Austin		B.P. Mann	B.P. Mann
Jan. 1879	E. Burgess		B.P. Mann	B.P. Mann
Jan. 1880	E. Burgess		B.P. Mann	B.P. Mann
Jan. 1881	E.L. Mark		B.P. Mann	B.P. Mann
Jan. 1882	S.H. Scudder		W. Trelease	W. Trelease
Jan. 1883	B.P. Mann		G. Dimmock	S. Henshaw
Jan. 1884	S.H. Scudder		G. Dimmock	B.P. Mann
Jan. 1885*	S.H. Scudder		G. Dimmock	B.P. Mann
Jan. 1886	S.A. Forbes		R. Hayward	B.P. Mann
Jan. 1887	J.H. Emerton		R. Hayward	B.P. Mann
Jan. 1888	W. Trelease		R. Hayward	S. Henshaw
Jan. 1889	S.H. Scudder		R. Hayward	S. Henshaw
May 1890	C.W. Woodworth		R. Hayward	S. Henshaw
Jan. 1891	G.H. Snow		R. Hayward	S. Henshaw
Jan. 1892	W.J. Holland		R. Hayward	S. Henshaw
Jan. 1893	W.H. Ashmead		R. Hayward	S. Henshaw
Jan. 1894	T.E. Beau		R. Hayward	S. Henshaw
Jan. 1895	C.M. Weed		R. Hayward	S. Henshaw
Jan. 1896	H.S. Pratt		R. Hayward	S. Henshaw
Jan. 1897	H.G. Dyar		R. Hayward	S. Henshaw
Jan. 1898	T.E. Beau		R. Hayward	S. Henshaw
Jan. 1899	A.G. Mayer		R. Hayward	S. Henshaw
Jan. 1900	J.W. Folsom		R. Hayward	S. Henshaw
Jan. 1901*	J.W. Folsom		R. Hayward	R. Hayward
Jan. 1902*	J.W. Folsom		R. Hayward	R. Hayward
Apr. 1903	A.P. Morse		W.L.W. Field	R. Hayward
Jan. 1904	J.H. Emerton		W.L.W. Field	R. Hayward
Jan. 1905	J.H. Emerton		J.W. Dow	R. Hayward
Jan. 1906	W.L.W. Field		A.H. Clark	R. Hayward
Jan. 1907	H.H. Newcomb		C.A. Frost	F.C. Bowditch
Jan. 1908	C.W. Johnson		C.A. Frost	F.A. Sherriff
Jan. 1909	P.G. Bolster	W.M. Wheeler	C.A. Frost	F.A. Sherriff
Jan. 1910	W.M. Wheeler	W.L. Fiske	C.A. Frost	F.A. Sherriff
Jan. 1911	L.W. Swett	W. Reiff	C.A. Frost	F.A. Sherriff
Jan. 1912	C.T. Brues	C.A. Frost	W.M. Mann	F.A. Sherriff
Jan. 1913	P.G. Bolster	J.W. Chapman	W.M. Mann	F.W. Dodge
Jan. 1914	A.P. Morse	J.W. Chapman	W.M. Mann	F.W. Dodge
Jan. 1915	C.W. Johnson	T. Barbour	H.M. Parshley	F.W. Dodge
Jan. 1916	A.F. Burgess	F.G. Carnochan	H.M. Parshley	F.W. Dodge
Jan. 1917	F.G. Carnochan	S.W. Denton	H.M. Parshley	C.A. Frost

*No elections at the annual meeting; officers held over.

Date of Election	President	Vice-President	Secretary	Treasurer
Jan. 1918	W.M. Wheeler	S.W. Denton	A.C. Kinsey	H.A. Preston
Jan. 1919	S.W. Denton	C.A. Frost	A.C. Kinsey	L.R. Reynolds
Jan. 1920	C.A. Frost	W.L.W. Field	J.H. Emerton	F.H. Walker
Jan. 1921	N. Banks	L.R. Reynolds	J.H. Emerton	F.H. Walker
Jan. 1922	W.M. Wheeler	L.R. Reynolds	J.H. Emerton	F.H. Walker
Jan. 1923	A.P. Morse	R.H. Howe	J.H. Emerton	F.H. Walker
Jan. 1924	C.T. Brues	R.H. Howe	J.H. Emerton	F.H. Walker
Jan. 1925	J.H. Emerton	C.W. Johnson	J.C. Bequaert	F.H. Walker
Jan. 1926	W.L.W. Field	O.E. Plath	J.C. Bequaert	F.H. Walker
Jan. 1927	O.E. Plath	S.M. Dohanian	F.M. Carpenter	F.H. Walker
Jan. 1928	J.C. Bequaert	F.M. Carpenter	J.W. Wilson	F.H. Walker
Feb. 1929	F.M. Carpenter	C.W. Collins	J.W. Wilson	F.H. Walker
Feb. 1930	F.M. Carpenter	C.W. Collins	R.P. Dow	F.H. Walker
Jan. 1931	C.A. Frost	C.W. Collins	P.J. Darlington, Jr.	F.H. Walker
May 1932	C.W. Collins	C.W. Johnson	J.W. Johnston	F.H. Walker
May 1933	A.P. Morse	P.J. Darlington, Jr.	M. Bates	F.H. Walker
May 1934	P.J. Darlington, Jr.	O.E. Plath	R.P. Dow	F.H. Walker
May 1935	J.C. Bequaert	O.E. Plath	D. Davenport	F.H. Walker
May 1936	O.E. Plath	F.M. Carpenter	D. Davenport	F.H. Walker
May 1937	C.A. Frost	J.C. Bequaert	V.G. Dethier	R.P. Dow
Oct. 1938	W.S. Creighton	C.H. Blake	V.G. Dethier	R.P. Dow
May 1939	C.H. Blake	F.M. Carpenter	C.T. Parsons	R.P. Dow
May 1940	F.M. Carpenter	P.J. Darlington, Jr.	R.P. Holdsworth	R.T. Holway
May 1941	P.J. Darlington, Jr.	J.C. Bequaert	C.M. Williams	R.T. Holway
May 1942	J.C. Bequaert	L.G. Wesson	G. Erikson	T. Rhyder
May 1943	N. Banks	C.T. Brues	G. Erikson	J.C. Bequaert
May 1944	C.T. Brues	K. Arbuthnot	G. Erikson	F.M. Carpenter
May 1945	C.T. Brues	K. Arbuthnot	G. Erikson	F.M. Carpenter
May 1946	P.J. Darlington, Jr.	J.C. Bequaert	N. Bailey	F.M. Carpenter
May 1947	G.A. Edwards	C.L. Remington	N. Bailey	F.M. Carpenter
May 1948	N. Bailey	W.L. Brown, Jr.	F.G. Werner	F.M. Carpenter
May 1949	F.G. Werner	W.L. Nutting	J. Woodland	F.M. Carpenter
May 1950	K. Christensen	A.G. Humes	R.J. Goss	F.M. Carpenter
May 1951	A.G. Humes	F.Y. Cheng	T. Eisner	F.M. Carpenter
May 1952	T. Eisner	W.L. Brown, Jr.	P.A. Adams	F.M. Carpenter
May 1953	W.L. Brown, Jr.	S.K. Harris	E.O. Wilson	F.M. Carpenter
May 1954	E.O. Wilson	T. Eisner	N.W. Gillham	F.M. Carpenter
May 1955	E.O. Wilson	P.A. Adams	R.H. Lippitt	F.M. Carpenter
May 1956	P.A. Adams	B.R. Headstrom	R.B. Willey	F.M. Carpenter
May 1957	R.B. Willey	S. Duncan	M.C. Parsons	F.M. Carpenter
May 1958	N. Gilham	M.C. Parsons	A.M. Stuart	F.M. Carpenter
May 1959	M.C. Parsons	A.L. Bull	A.M. Stuart	F.M. Carpenter
May 1960	H.W. Levi	N. Bailey	G.L. Bush	F.M. Carpenter
May 1961	J.J.T. Evans	C. Walcott	A.R. Brady	F.M. Carpenter

Date of Election	President	Vice-President	Secretary	Treasurer
May 1962	L.M. Roth	A.R. Brady	E.G. MacLeod	F.M. Carpenter
May 1963	E.G. MacLeod	J. Beatty	J. Reiskind	F.M. Carpenter
May 1964	R.W. Taylor	J. Reiskind	H. Reichardt	F.M. Carpenter
May 1965	H. Reichardt	S. Vogel	C.C. Porter	F.M. Carpenter
May 1966	J. Reiskind	C.C. Porter	F.C. Coyle	F.M. Carpenter
May 1967	F.C. Coyle	R.W. Matthews	L. Pinter	F.M. Carpenter
May 1968	W.G. Eberhard	C.F. Moxey	S.B. Peck	F.M. Carpenter
May 1969	S.B. Peck	R.E. Silberglied	W. Shear	F.M. Carpenter
May 1970	R.E. Silberglied	C.F. Moxey	C.S. Henry	F.M. Carpenter
May 1971	C.S. Henry	T.P. Webster III	H.F. Nijhout	F.M. Carpenter
May 1972	F. Nijhout	T.H. Hlavac	R. Swain	F.M. Carpenter
May 1973	B. Hölldobler	W.D. Winter	H.E. Nipson	F.M. Carpenter

EDITORS OF PSYCHE

Volume	Years	
1	1874-76	B. Pickman Mann
2	1877-79	George Dimmock and B. P. Mann
3	1880-82	George Dimmock and B. P. Mann
4	1883-87	George Dimmock and B. P. Mann
5	1888-90	George Dimmock and Samuel Henshaw
6	1891-93	Samuel Henshaw
7	1894-96	Samuel Henshaw
8	1897-99	Samuel Henshaw
9	1900-02	Samuel Henshaw
10	1903	Samuel Henshaw
11	1904	W. L. W. Field
12	1905	W. L. W. Field
13	1906	W. L. W. Field
14	1907	W. L. W. Field
15	1908	W. L. W. Field
16	1909	W. L. W. Field
17	1910	Charles T. Brues
↓	↓	↓
53	1946	Charles T. Brues
54	1947	Frank M. Carpenter
↓	↓	↓
81	Present	Frank M. Carpenter

SUPPLEMENTARY STUDIES ON ANT LARVAE: TERATOMYRMEX[1]

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The first collector of this Australian genus, T. Greaves, Esq. (in 1942), must have been surprised when he first viewed his specimens under magnification; he probably thought he had collected diseased ants. The describer (J. J. McAreavey 1957) was evidently somewhat astonished for he gave it the name *Teratomyrmex,* from the Greek *teras* (*teratos*) monster, marvel, wonder + *myrmex* ant. We have in English *teratism* the worship of monsters, *teratology* the study of monstrosities and *teratoma* a tumor derived from more than one embryonic layer and made up of a mixture of tissues. *Teratomyrmex* is certainly an appropriate name, for the worker looks as if it has a huge tumor on the top of its thorax (see Fig. 7 and 8). Aside from this unique peculiarity the genus is quite ordinary and belongs in the Formicini, an ordinary tribe of Formicinae, which includes such anatomically commonplace genera as *Acanthomyops, Lasius* and *Formica.*

The first specimens of *Teratomyrmex* we have seen were a gift from Rev. B. B. Lowery (of Norwood, South Australia) in 1967. In the accompanying letter he wrote: "I have also taken the liberty of filling up the vacant spaces in the box with a few specially chosen mountings for your collection. Make sure you have a look at the *Teratomyrmex* and *Epopostruma frosti* under the microscope. Both these species, by the way, are very rare." In a later note he wrote: "The species [*T. greavesi*] appears to be rare in the ranges near Murwillumbah NE. NSW. Forages on low shrubs and in leaf litter. Nests in very moist places, usually in white-rotten timber. It is very easily mistaken for a small black *Iridomyrmex.*" He also included a quotation from a personal communication he had received from Tom Greaves: "'*T. greavesi* is a dominant ant in residual forest,' i.e., in the Jackall Ranges, about 75 miles north of Brisbane."

[1]Hymenoptera: Formicidae: Formicinae.

Manuscript received by the editor December 10, 1973

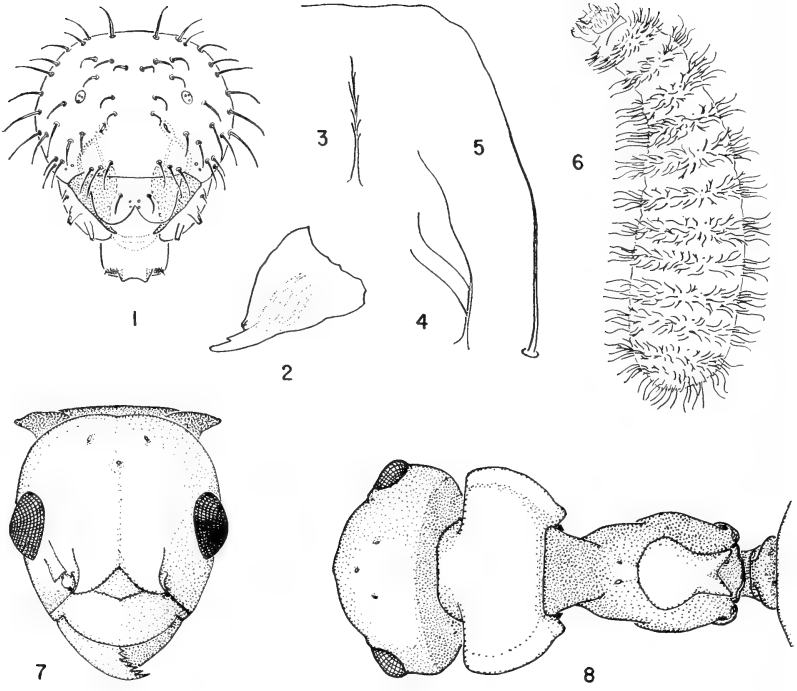
Recently Dr. W. L. Brown sent us a worker of *Teratomyrmex* (see Fig. 7 and 8) together with several larvae. Given such a weird worker could one reasonably expect its larva to be somewhat bizarre also? We hoped it would. And we were disappointed: the larva is quite ordinary. Its profile is pogonomyrmecoid, a character shared with 19 other genera in the Formicinae; its mandibles are camponotoid in common with 23 other formicine genera. In fact, in our key to the larvae of the Formicidae (1974), in which most ant larvae were differentiated to genera or at least to tribes, we could only add *Teratomyrmex* to the residual lump of 22 undifferentiated genera: "Tribes Formicini, Gesomyrmecini, Gigantiopini, Melophorini and Plagiolepidini."

The index of specialization (see our 1974) for *Teratomyrmex* is 14; that of the tribe Formicini is 14. [The most specialized ant larvae — the Leptanillinae — have an index of 35, while the Formicinae as a whole are less specialized with 17. The index for the family as a whole is 22.]

Genus Teratomyrmex McAreavey

Body pogonomyrmecoid. Entire integument spinulose. Body hairs long and moderately numerous; of 3 types: denticulate; long, smooth and flexuous; 2- or 3-branched, smooth with the branches long and flexuous. Head hairs moderately numerous; unbranched, denticulate throughout most of length. Labrum deeply bilobed. Mandibles camponotoid. Maxillae with paraboloidal apex; palp a paxilla; galeae digitiform. Labrum subrectangular in anterior view; palp a short paxilla; opening of sericteries wide and salient.

Teratomyrmex sp. (near *greavesi* McAreavey) Fig. 1-6. Length (through spiracles) about 3.7 mm. Shape pogonomyrmecoid (i.e., diameter greatest near the middle of the abdomen, decreasing gradually toward head and more rapidly toward posterior end, which is rounded; thorax more slender and forming a rather stout neck which is curved ventrally) but abdomen rather slender. Anus posteroventral and with 2 small lips. Wing and gonopod vestiges present. Ten pairs of spiracles. Entire integument spinulose, the spinules most prominent on the venter of T1-3 and AI-AIII, sparse and scattered elsewhere. Body hairs moderately numerous and long. Of 3 types: (1) 0.075-0.15 mm long, unbranched and with numerous short denticles, longest and most numerous on the thorax; (2) 0.2-0.33 mm long, unbranched, smooth, very long, slender and flexuous, none on



Textfigure 1-6, larva. 1, head in anterior view, ×71; 2, left mandible in anterior view, ×145; 3-5, three types of body hairs ×267; 6, larva in side view, ×14.

Textfigure 7 and 8, worker. 7, head and dorsum of pronotum in anterior view, ×34; 8, head, thorax and petiole in dorsal view, ×34.

T1, more numerous on abdomen; (3) 0.09-0.15 mm long, 2- or 3-branched, with long slender tips, on all somites. Cranium suboctagonal; broader than long. Antennae small, each a slight elevation with 3 sensilla, each of which bears a small spinule. Head hairs moderately numerous, rather long (0.05-0.09 mm) and rather stout, unbranched and with numerous fine denticles throughout length. Mouth parts large. Labrum bilobed; each lobe with 2 hairs about 0.05 mm long with small denticles and with 5 sensilla on and near the ventral border; posterior surface spinulose, the spinules in short to long rows, the rows radiating from each dorsolateral angle, and with 5 sensilla on each half near the midline. Mandibles camponotoid (i.e., subtriangular; base broad, width 2/3 length; apex forming a round-pointed tooth; one small subapical tooth); anterior and posterior surfaces with numerous short longitudinal rows of minute spinules. Maxillae with the apex paraboloidal; palp a paxilla with 5 (3 apical and bearing a spinule each, 1 subapical and encapsulated, 1 lateral and bearing a spinule) sensilla; galea digitiform, with 2 apical sensilla. Labium subrectangular in anterior view; anterior surface with minute spinules in short rows; palp a short peg with 5 (3 apical and bearing a spinule each and 2 lateral — 1 encapsulated and 1 bearing a spinule) sensilla; opening of sericteries wide and salient, with 2 ventral projections. Hypopharynx densely spinulose, the spinules minute and arranged in numerous subparallel rows; the rows grouped in 2 subtriangles which have their bases near the middle.

Material studied: 14 larvae from Queensland: Cedar Creek Falls, Tamborine Mts., Ross & Cavagnaro, 1962; courtesy of Dr. W. L. Brown.

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MODIFICATION OF THE INTERSEGMENTAL REGION IN THE PTEROTHORAX OF *CRYPHOCRICOS* (HETEROPTERA: NAUCORIDAE)*

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Introduction

In most Hydrocorisae (aquatic Heteroptera) the hindlegs are used for swimming, and their extrinsic muscles, which originate in the metathorax, are well developed. The tergal and pleural depressors of the metathoracic trochanter (Muscles 70 and 71, respectively, of Larsén, 1945) are especially large in many Hydrocorisae, including the Naucoridae (Larsén, 1945) and the closely related family Aphelocheiridae (Parsons, 1969). These muscles slant anterolaterally in the metathorax, their anteriormost fibers originating near its boundary with the mesothorax.

In at least three genera of Naucoridae (*Limnocoris, Ambrysus,* and *Cryphocricos*) the anterior part of the metathoracic episternum, on which Muscle 71 originates, usually projects into the cavity of the preceding segment. This makes it appear, at first glance, that the anteriormost fibers of the muscle attach on the mesothorax. The metapleural projection, which will be described in a later publication, appears to be produced by post-ecdysial growth of the skeleton, since it is absent in newly-moulted adults and is present only in older ones.

Another example of post-ecdysial skeletal change occurs in the tergum of adult *Cryphocricos barozzii* and makes the anteriormost fibers of Muscle 70 appear to originate on the mesothorax rather than on the metathorax. This tergal modification seems to occur only in micropterous specimens, with reduced forewings. I have not observed it in macropterous *Cryphocricos* or in *Ambrysus, Limnocoris,* or *Pelocoris,* all of which possess forewings of normal length.

Materials and Methods

Cryphocricos barozzii Signoret, collected in Nova Teutônia, Brazil, and preserved in 70% alcohol, were dissected in 80% alcohol under

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a stereoscopic microscope. The attachment of Muscle 70 was studied by cutting the tergum sagittally, with a razor blade; the cut was made half way between the ventral phragmal process and the base of the mesothoracic wing. A few *Pelocoris femoratus* Palisot-Beauvois, preserved in Bouin's fluid, were also examined for comparison.

Most of the *Cryphocricos* were micropterous, lacking hindwings and indirect flight muscles and possessing forewings which reached only as far as the third abdominal segment. Only two of the rare macropterous forms, with forewings and hindwings extending nearly to the tip of the abdomen, were available for the investigation. Although they were not extensively dissected, their indirect flight muscles appeared to be either degenerate or absent.

Newly-moulted *Cryphocricos* could be distinguished from older individuals by the thinness of their exoskeletons and by the distinctness and relative thickness of the underlying epithelial layer. In older specimens the epithelium was thinner, less distinct, and easily torn, and the thickened exoskeleton had a layered appearance, probably owing to the deposition of successive internal layers of endocuticle after ecdysis, as Neville (1970) has observed in several insects. These layers could be peeled away from each other in an older specimen of *Cryphocricos* which had been immersed for 24 hours in a concentrated solution of potassium hydroxide.

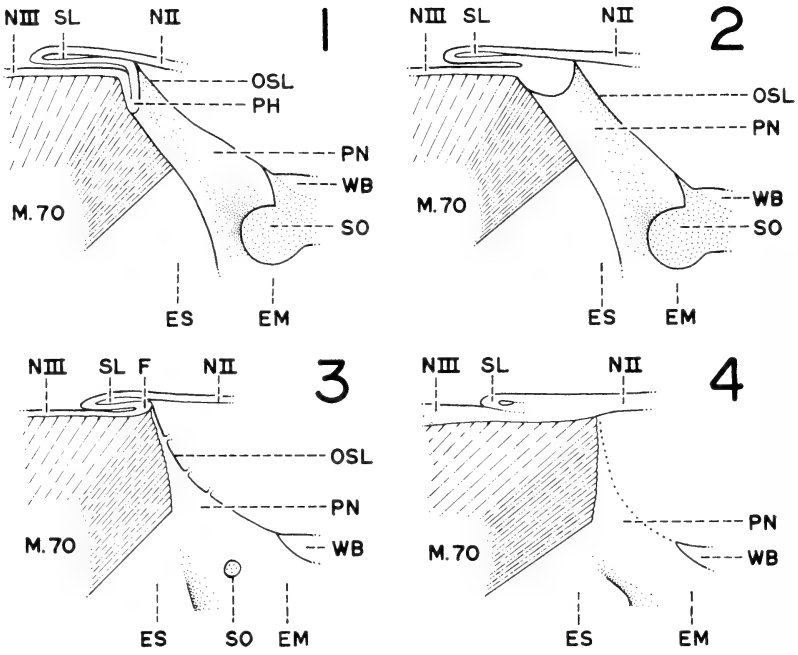
Observations

Typical Naucoridae

(figs. 1, 5)

In most macropterous naucorids, such as *Pelocoris,* the posterior margin of the mesothoracic notum (fig. 1; N II) is evaginated, forming a double-walled scutellar lobe (SL). The opening into the lobe (OSL) extends anterolaterally to the base of the forewing (WB). Immediately ventral to this opening lies the well developed mesothoracic postnotum (PN), which bears the second phragma (PH). The postnotum separates the metathoracic notum (N III) from the scutellar lobe and is mostly concealed by the latter externally. Only its most lateral part, which joins the mesothoracic epimeron (EM), forming a postalar bridge, is externally visible. The postalar bridge bears a large sensory membrane (SO), part of the mesothoracic scolopophorous organ (Larsén, 1957).

The concealed medial portion of the postnotum forms a two-walled, vertical invagination, the second phragma (PH). The



Figures 1-4, Diagrammatic internal views of dorsolateral intersegmental region of pterothorax in various adult Naucoridae. Left side of body has been cut parasagittally through terga (cut edge), between ventral phragmal process (not shown) and wingbase (WB). Fig. 1. Typical macropterous Naucoridae (based on *Pelocoris femoratus*). Fig. 2. Macropterous *Cryphocricos barozzii*. Fig. 3. Newly-moulted micropterous *C. barozzii*. Fig. 4. Older micropterous *C. barozzii* (dotted line indicates approximate position of opening into scutellar lobe, which is no longer visible).

phragma is especially pronounced on either side of the midline, where it bears a pair of large ventral processes (fig. 5; VP) upon which two of the mesothoracic indirect flight muscles attach (Muscles 30 and 31 of Larsén, 1945; present but degenerate in most *Pelocoris*).

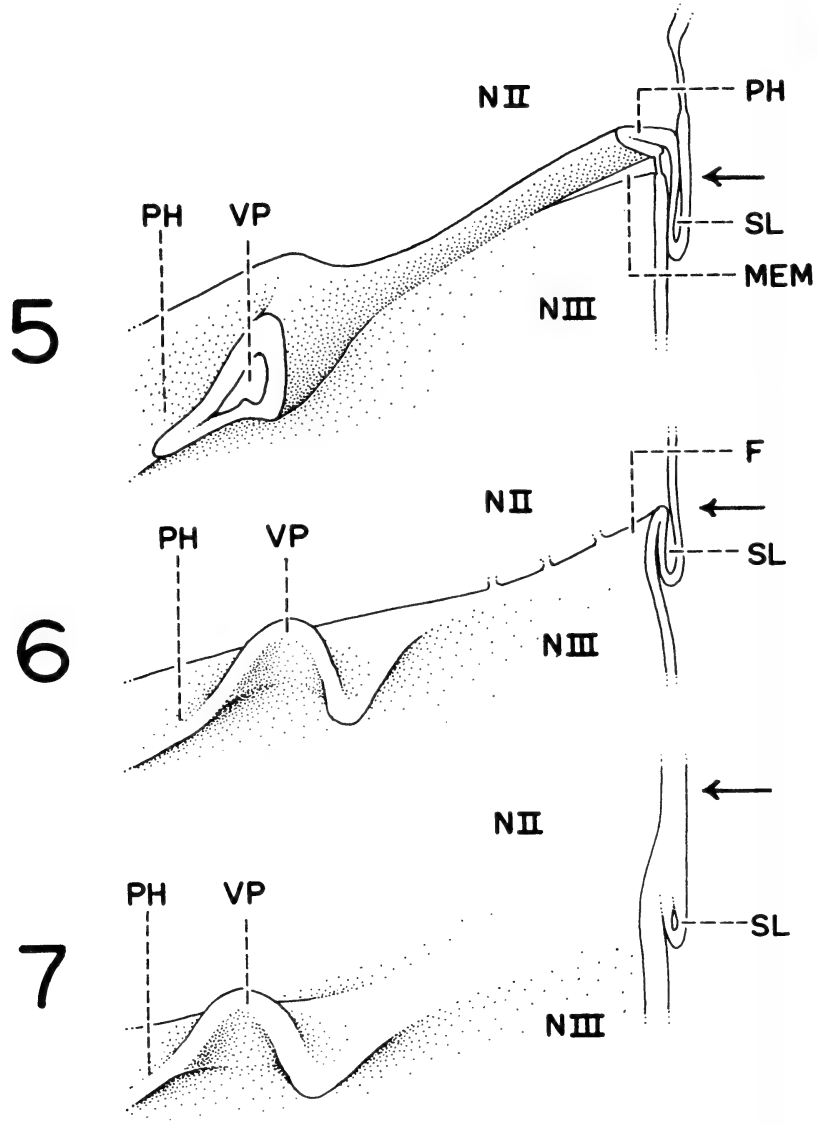
According to Snodgrass (1935) the phragma represents the primary boundary (antecosta) between the metathorax and mesothorax, and the mesothoracic postnotum is thus an intersegmental plate which is only secondarily associated with the mesothorax. This interpretation, which has been challenged by Matsuda (1970), is supported by the fact that the posterior wall of the phragma is continuous with the metathoracic episternum (fig. 1; ES).

Muscle 70 (fig. 1; M. 70) originates posterior to the phragma and postnotum, its fibers attaching only on the metathoracic notum. The latter forms a sharp angle with the posterior wall of the phragma. The angle is sclerotized medially (fig. 1) but contains a narrow membrane laterally (fig. 5; MEM). The membrane lies immediately anterior to the origin of Muscle 70.

Macropterous *Cryphocricos* (fig. 2)

Most of the typical structural relationships described above are also present in macropterous *Cryphocricos.* In the latter, however, the postnotum forms a definite, double-walled second phragma only near the midline, at and between the ventral processes (position same as in micropterous *Cryphocricos,* figs. 6, 7). Lateral to the ventral processes the postnotum does not seem to be invaginated, and appears merely as a transverse thickening (fig. 2, PN) just posteroventral to the opening into the scutellar lobe (OSL). Neither of the two available macropterous specimens were newly-moulted. It is thus possible that a low, double-walled phragmal invagination is present in this region immediately after ecdysis. As new layers of endocuticle are subsequently laid down, the structure of the phragma could become obscured, giving it the appearance of an uninvaginated thickening in older specimens.

Laterally the anterior portion of the postnotal thickening forms a well-defined postalar bridge with the mesothoracic epimeron (EM). The bridge contains a large sensory membrane (SO) similar to that of typical naucorids. The posterior portion of the postnotal thickening is continuous laterally with the metathoracic episternum (ES) and medially with the metanotum (N III). Its boundary with the


5
NII
PH
PH
VP
SL
MEM
NIII
6
F
NII
PH
VP
SL
NIII
7
NII
PH
VP
SL
NIII

latter is marked dorsolaterally by a narrow, unpigmented band of sclerotization, the homologue of the membrane (fig. 5; MEM) which is present in typical Naucoridae. Muscle 70 originates only on the metanotum, posterior to this band, as in other macropterous naucorids, and its fibers do not extend onto the postnotum (fig. 2).

Micropterous *Cryphocricos* (figs. 3, 4, 6, 7)

In short-winged *Cryphocricos,* as in macropterous ones, a well-defined second phragma (figs. 6, 7; PH) is present only at and between the ventral phragmal processes (VP). In addition, the mesothoracic postnotum appears to be incomplete in micropterous *Cryphocricos.* These skeletal modifications are more easily observed in newly-moulted adults (figs. 3, 6) than in older ones in which parts of the thickened exoskeleton have coalesced (figs. 4, 7).

In newly-moulted specimens the portion of the postnotum which usually lies immediately lateral to the ventral phragmal processes appears to have disappeared. The scutellar lobe (figs. 3, 6; SL) is shorter than in macropterous *Cryphocricos,* and its ventral wall is directly continuous medially with the metanotum (N III), upon which Muscle 70 originates. The junction between these two regions forms a fold (F) which projects anteriorly and is continuous with the phragmal process (fig. 6). Short, sclerotized struts connect its edge secondarily with the mesonotum (N II). The anteromedial fibers of Muscle 70 originate on the edge of this fold, immediately beneath the opening into the scutellar lobe (fig. 3; OSL). They thus attach farther anteriorly than in macropterous *Cryphocricos* (fig. 2), in which they originate well posterior to the opening.

The more anterolateral fibers of Muscle 70 do not attach to the edge of the fold but are separated from it by a roughly triangular area which represents the lateral portion of the incomplete postnotum (fig. 3; PN). There is no membrane or unpigmented band marking its posterior boundary with the metanotum. It is ventrally continu-

Figures 5-7, Diagrammatic internal views of intersegmental part of pterothoracic terga in various adult Naucoridae. Terga have been cut parasagittally, medial to wingbases, and removed from body; only left side, between ventral phragmal process (VP) and cut edge, is shown. Arrow indicates level at which anteriormost fibers of Muscle 70 originate. Fig. 5. *Pelocoris femoratus* (ventral phragmal process cut off at base). Fig. 6. Newly-moulted micropterous *Cryphocricos barozzii.* Fig. 7. Older micropterous *C. barozzii.*

ous with the mesothoracic epimeron (EM), and the postalar bridge contains a very reduced scolopophorous organ (SO).

In older micropterous *Cryphocricos* skeletal boundaries are much more difficult to interpret, owing to the thickening of the cuticle, the differential growth of some regions, and the obliteration of folds, making them appear as solid thickenings rather than hollow invaginations or evaginations. Comparison of older specimens (fig. 4) with newly-moulted ones (fig. 3) indicates that during post-ecdysial development several changes have occurred in the lateral and dorsolateral intersegmental region of the pterothorax. The scolopophorous sense organ is no longer visible on the internal surface of the postalar bridge. The cavity of the scutellar lobe (fig. 4; SL) has been reduced, and the opening into the lobe (fig. 4; dotted line) is no longer visible. The ventral wall of the lobe merges indistinguishably with the fold which borders on it ventrally. In newly-moulted *Cryphocricos* this well-defined fold (fig. 3; F) marks the boundary of the scutellar lobe with the metanotum medially (fig. 3; cut edge) and with the postnotum laterally (PN). In older adults these boundaries have become obscured. The fold and scutellar lobe appear as three separate layers only posteriorly; more anteriorly they appear as a single, somewhat thickened layer (fig. 4).

In addition, the anteromedial fibers of Muscle 70, which originate on the metanotum, attach considerably more anteriorly in older *Cryphocricos* than in younger ones (figs. 3, 4; M. 70; figs. 6, 7; arrows). This suggests that the fold (figs. 3, 6; F) between the scutellar lobe and the metanotum grows anteriorly as new layers of endocuticle are added to the internal surface of the skeleton. One older specimen, in which the muscle attached at the level indicated by the arrow in Figure 7, was treated in potassium hydroxide so that the more internal layers of endocuticle could be peeled away from the outermost ones. Although the inner layers lacked a fold, the more external ones showed a definite one which lay posterior to the level at which the muscle fibers had originated.

Discussion

In these descriptions I have taken the view that Muscle 70 originates on the metanotum in all four types of Naucoridae. In the two macropterous forms (figs. 1, 2) its origin is separated from the mesoscutellar lobe by the postnotum. In micropterous *Cryphocricos* (figs. 3, 4), however, a portion of the postnotum, immediately lateral to the

ventral phragmal process, is absent. In this region, consequently, the part of the metanotum on which Muscle 70 originates borders directly on the scutellar lobe. This atypical intersegmental boundary appears to grow anteriorly during post-ecdysial development.

Figures 3 and 4 could be interpreted in two other ways, either (1) that there are no post-ecdysial changes in skeletal boundaries and that in Figure 4 the anteriormost fibers of Muscle 70 have simply shifted anteriorly, onto the mesonotum, or (2) that a postnotum is present lateral to the phragmal process and is represented by the fold (fig. 3; F) upon which the anteromedial fibers of Muscle 70 attach. According to this second view the origin of the muscle has shifted from the metanotum onto the homologue of the thickened postnotum of macropterous *Cryphocricos* (fig. 2; PN). Consequently, it is the boundary between the mesothoracic scutellum and postnotum (secondary intersegmental boundary of Snodgrass, 1935) which appears to grow anteriorly after ecdysis, rather than a primary intersegmental boundary. Neither of these two interpretations has been adopted here because in *Cryphocricos* and at least two other genera of Naucoridae post-ecdysial skeletal growth takes place in the pterothoracic pleuron (see p. 46) and almost certainly occurs along the primary intersegmental boundary between the metathoracic episternum and the mesothoracic epimeron.

Degeneration or absence of the three mesothoracic indirect flight muscles, and consequent loss of the ability to fly, is a common occurrence among Hydrocorisae (Larsén, 1950). Extreme alary dimorphism such as that of *Cryphocricos* is much less common. Larsén (1950) studied *Aphelocheirus* (Aphelocheiridae) which has both micropterous and macropterous forms, and found that the size and shape of the ventral phragmal processes, upon which two of the indirect flight muscles attach, differ in the two types. Similar differences in the phragmal processes occur in flying and flightless *Ilyocoris* (Naucoridae; Larsén, 1970). Both forms of *Ilyocoris* possess forewings and hindwings of normal length, but most individuals lose their indirect flight muscles soon after the final moult. Larsén did not, however, observe post-ecdysial skeletal changes, absence of the lateral part of the second phragma, or loss of a portion of the mesothoracic postnotum in either *Aphelocheirus* or *Ilyocoris*. All these features appear to occur in micropterous *Cryphocricos*.

Acknowledgements

I wish to thank Fritz Plaumann (Nova Teutônia, Brazil) for

collecting the *Cryphocricos,* John Polhemus (Englewood, Colorado) for identifying them, my husband, Thomas Parsons, for examining the manuscript, and Donald Chant and the Department of Zoology, University of Toronto, for making available the laboratory facilities for this research. The investigation was made possible by a grant from the National Research Council of Canada.

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THE POLYTYPIC GENUS *CELOTES* (LEPIDOPTERA: HESPERIIDAE: PYRGINAE) FROM THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO*

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Although most species of American hesperiids are hard to determine, some are not; and none is more immediately distinct than the "streaky skipper," *Celotes nessus* (Edwards). Ever since it was described (in genus *Pholisora*) in 1877, nothing else like it has been known. Indeed, since the turn of the century — despite abortive attempts of various workers to jam it into polytypic genera (such as *Pyrgus* [then commonly called *Hesperia*], *Systasea,* and *Antigonus*) — it has properly stood alone in the monotypic genus *Celotes* (Godman and Salvin 1899). I feel, therefore, a measure of remorse in now describing a second species of *Celotes* that closely resembles the first.

Although I have accumulated data on *Celotes* since New Year's Eve of 1961, when I first recognized it as polytypic, I still see no clear clues to the evolutionary differentiation of *C. nessus* and the species to be described: they overlap fully in space and in time, and at least partly in choice of larval foodplants. The new species is a multivoltine mallow-eater occurring in a montane strip that runs northwest-southeast through the middle of the range of *C. nessus.*

Because *C. nessus* is both peculiar and familiar, the following description is comparative. And because original descriptions can be too tedious for words, this one is largely visual.

In preparing it, I have examined the genitalia of all specimens of *Celotes* available to me and possessed of an abdomen — a total of 529 individuals, of which 97 represent the new species. Wherever possible, I have also examined the metathoracic pouch of males. Each pinned specimen studied has received a sex-and-determination label.

The new specific name is a noun in apposition.

Celotes limpia new species

Holotype. — ♂, Limpia Canyon, 5000 feet, Davis Mountains, 4 miles WNW of Fort Davis, Jeff Davis County, Texas, May 2,

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1959 (J. M. and S. N. Burns) [Museum of Comparative Zoology no. 31888].

Size. — On average, *limpia* is larger than *nessus;* and, in both species, females are larger than males, although size varies considerably (table 1). In *nessus,* the wingspread of Texas specimens exceeds that of Arizona specimens by at least 1 mm.

Table 1. Maximum wingspread in well-mounted specimens of *Celotes* from Texas.

Species	Sex	Number measured	Wingspread (mm) Mean	Range
nessus	♂	35	23.7	22-26
"	♀	22	25.1	23-27
limpia	♂	39	25.9	23-29
"	♀	24	27.8	25-31

Facies. — Fig. 1E-H. Very like *nessus* (fig. 1A-D), but with slightly larger and more conspicuous hyaline spots and a generally paler aspect.

Noteworthy in the latter connection is a set of pale areas between dark marks on the proximal 60% of the ventral secondary (i.e. from the three hyaline spots of the secondary inward): these pale areas are enlarged and whitened in *limpia* and hence usually more pronounced than in *nessus.* In dorsal view, unworn (particularly reared) specimens of *limpia* may show considerable grayish overscaling on the body and adjacent wing bases. The usually paler shades of brown and tan in *limpia* tend to make it reflect more and appear colder and harder and sometimes more contrasty. All of these average differences involving color are perceptible chiefly when *limpia* is compared with *nessus* from Texas; *nessus* from Arizona (where *limpia* does not occur) often essentially duplicates the facies of *limpia* — except insofar as the remarkably small average size of Arizona *nessus* gives its pattern a special sharpness. Wear and fading

Data for specimens in Fig. 1:

A, B — Sitting Bull Falls, 4650 feet, Guadalupe Mountains, Eddy County, New Mexico, V-26-1959 (J. M. and S. N. Burns).

C, D — Topotype. San Antonio, Bexar County, Texas, VI-30-1963 (J. M. Burns).

E, F — Holotype. Limpia Canyon, 5000 feet, Davis Mountains, 4 mi. WNW of Fort Davis, Jeff Davis County, Texas, V-2-1959 (J. M. and S. N. Burns).

G, H — Allotype. As for holotype, except V-1-1959.

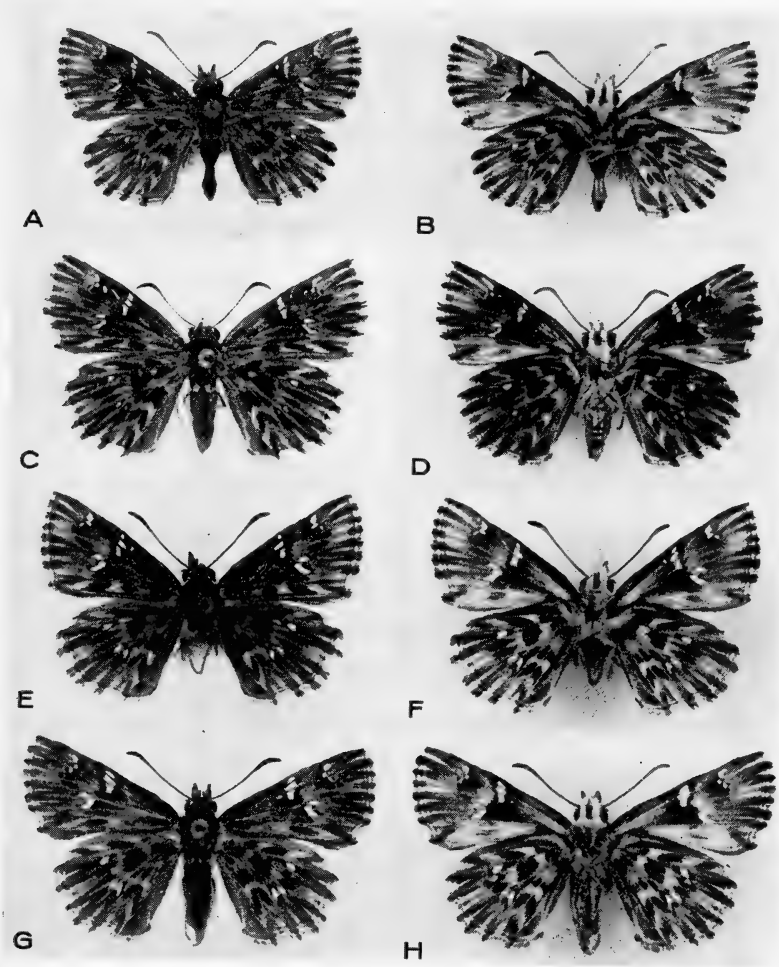

Fig. 1. Facies of *Celotes*.

C. nessus	A	B	→	♂
	C	D	→	♀
C. limpia	E	F	→	♂
	G	H	→	♀
	↓ dorsal	↓ ventral		

raise additional hell with these subtle color characters, but no matter: the genitalia (q.v.) last and last.

Male scent-spreading sex characters. — Males of *limpia,* like those of *nessus,* have a narrow costal fold on the primary and a metathoracic system of ventral pouch and tibial tufts. The metathoracic pouch of *limpia* (fig. 2B) bears short linear scales over most or all of its dorsal surface (except at the lateral margin). In *nessus* (fig. 2A), linear scales are altogether absent (particularly in Arizona males) or, if present (as in Texas males), are much less dense and/or proximal in distribution; even in extreme cases, they never attain the distal apex of the pouch, and the pouch is therefore clad —-entirely or for its greater part — with much broader, flat-lying shinglelike scales (cf. figs. 2A and 2B). Because the linear scales of *limpia* are creamy, whereas some to all of the broad shinglelike scales of *nessus* are gray to brown, the general color of the dorsal surface of the metathoracic pouch differs in the two species. (Interior morphology of costal folds has not been studied.)

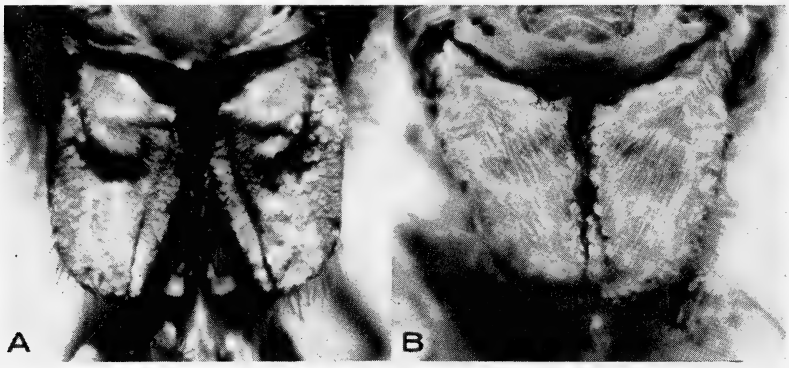

Fig. 2. Metathoracic pouch of the male; abdomen removed, dorsoposterior view. A. *Celotes nessus* from Austin, Travis County, Texas, V-26-1966 (J. M. Burns). B. *Celotes limpia,* a paratype reared out IX-10-1966 from a larva collected on *Abutilon malacum,* 15 mi. SE Redford, 2500 ft., Presidio County, Texas, VIII-18-1966 (R. O. Kendall).

Male genitalia. — Fig. 4. Although basically similar to *nessus* (fig. 3), there are abundant differences, of which the most salient include the following. (1) In *limpia,* a long thin flattened projection, like a curved spatula, arises from the dorsoposterior rim of the body of the valva and starts dorsad but at once curves caudad, extending far back to become the caudalmost valval element and to end in a

slightly flared tip with a peripheral array of fine sharp teeth (fig. 4A-C). Its homolog in *nessus* is a robust spike arising in a similar position, except that the distinctive high dorsal curvature of the body of the valva in *nessus* places the origin of the spike well down on the medial surface of the valva (fig. 3A-C); this tapering spike extends chiefly dorsad, but usually bends slightly caudad at its apex, which is pointed and often entire or bifurcate (fig. 3A,B), but sometimes trifurcate, or very rarely quadrifurcate; although occasionally broadened or lengthened and bent strongly caudad apically, the spike *never* approaches the form of the spatula in *limpia.* (2) Anterior end of tegumen, in *limpia,* large and well-developed, projecting far cephalad (fig. 4E,F); but in *nessus,* extraordinarily reduced (fig. 3E,F). (3) In *limpia,* uncus broad, and the paired terminal prongs of the uncus heavy and stubby (fig. 4F); but in *nessus,* uncus relatively narrow, and its terminal prongs more delicate (fig. 3F).

Female genitalia. — Fig. 6. Sterigma of *limpia* altogether more massive (fig. 6A,B) and, viewed ventrally, more nearly square in outline (fig. 6A); heavy central sclerotization in lamella postvaginalis like a wide triangle tapering quickly toward ostium bursae (fig. 6A). Sterigma of *nessus* (fig. 5) less massive (fig. 5A,B) and, in ventral view, narrower posteriorly, suggesting in outline a caudally truncated triangle (fig. 5A) more than a square; heavy central sclerotization in lamella postvaginalis limited to a comparatively narrow midventral strip that tapers but little toward ostium bursae (fig. 5A). Ostium bursae of *limpia* a relatively narrow curved slit, like a crescent bowed dorsad (fig. 6C), but that of *nessus* large and more or less round, like a manhole (fig. 5C).

Spatial distribution. — A widespread species, *nessus* ranges from about the 97th meridian in southcentral Oklahoma and central Texas west to northwestern and southeastern Arizona and south in Mexico to at least southern Sonora, southern Chihuahua and Coahuila (fig. 7). By contrast, so far as known, *limpia* occurs only along the southern Rocky Mountain axis in Trans-Pecos Texas and along the Mexican counterpart of this axis, the northern segment of the Sierra Madre Oriental, as far south at least as southern Coahuila (fig. 8). Having been taken in numbers in the Guadalupe, Davis, and Chisos mountains of Trans-Pecos Texas, *limpia* may confidently be expected (1) in many other west Texan ranges — such as the Delawares, Chinatis, and Santiagos — that are more or less associated with the scattered southern Rocky Mountain system, (2) northward in at least the New Mexican extension of the Guadalupes, if not in the Sacramentos and more northern chains, and (3) southward in Chi-

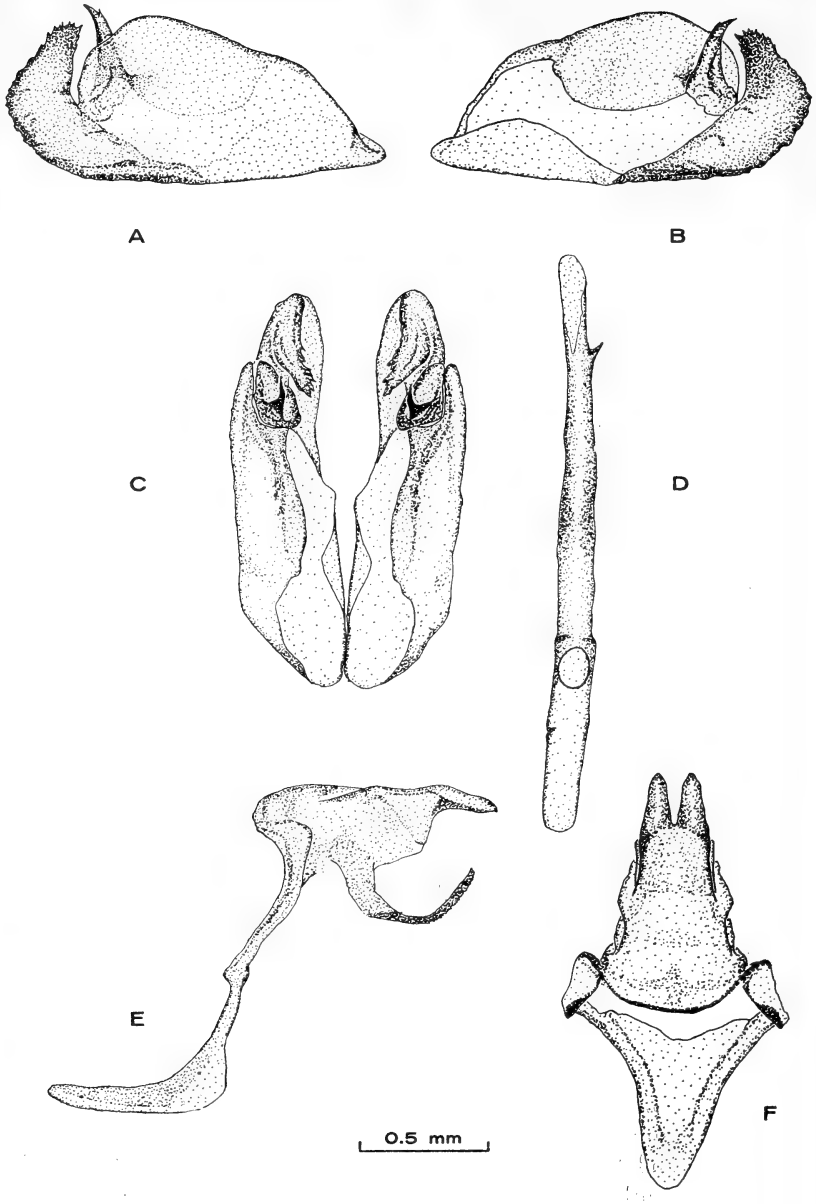

Fig. 3. Male genitalia of *Celotes nessus*. A. Lateral view of right valva. B. Medial view of right valva. C. Dorsal view of both valvae. D. Dorsal view of aedeagus. E. Left lateral view of uncus, tegumen, gnathos, vinculum, and saccus. F. Dorsal view of uncus, tegumen, vinculum, and saccus. [A and B, drawn from male from Palo Duro Canyon, 2800 feet, Randall County, Texas, V-10-1959 (J. M. and S. N. Burns); C to F, from male from Austin, Travis County, Texas, V-26-1966 (J. M. Burns).]

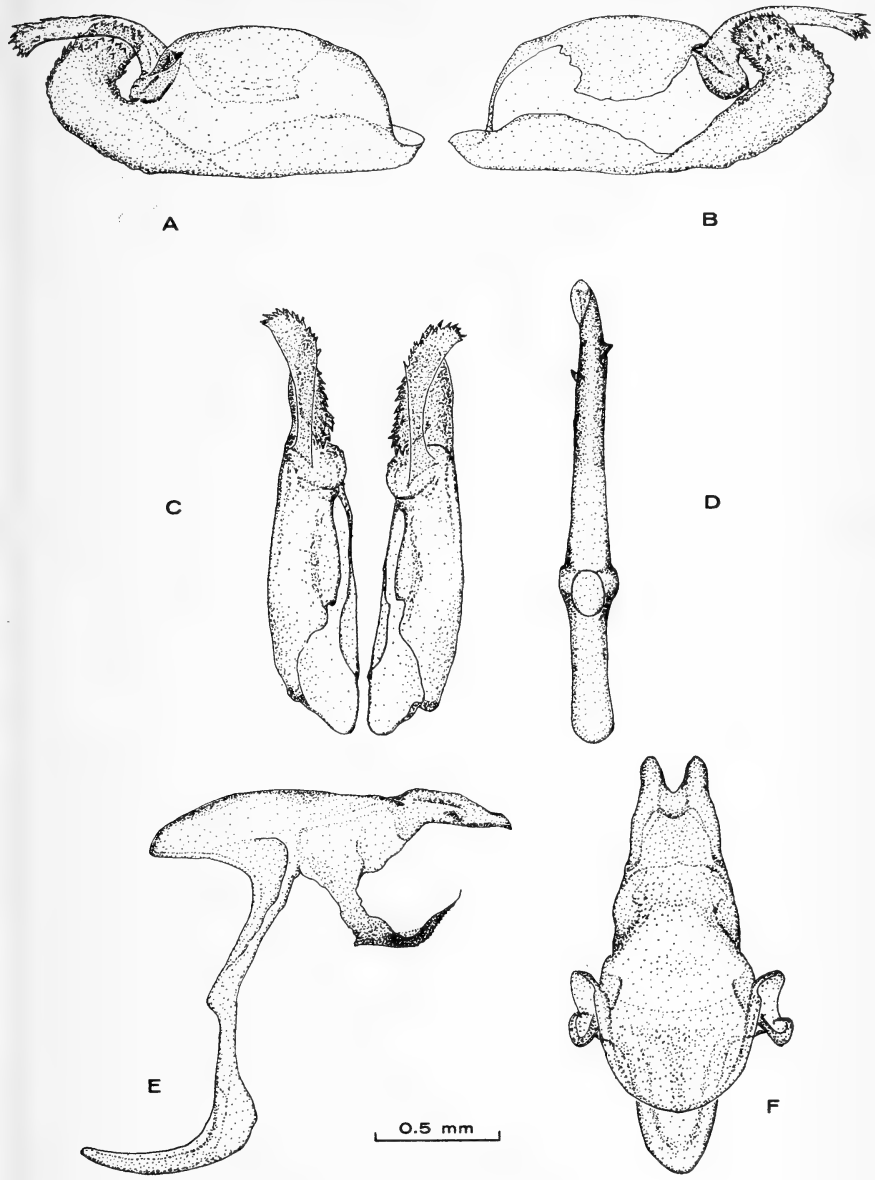

Fig. 4. Male genitalia of *Celotes limpia*. A to F as in fig. 3. [A and B, drawn from holotype; C to F, from paratype from type locality, V-4-1959 (J. M. and S. N. Burns).]

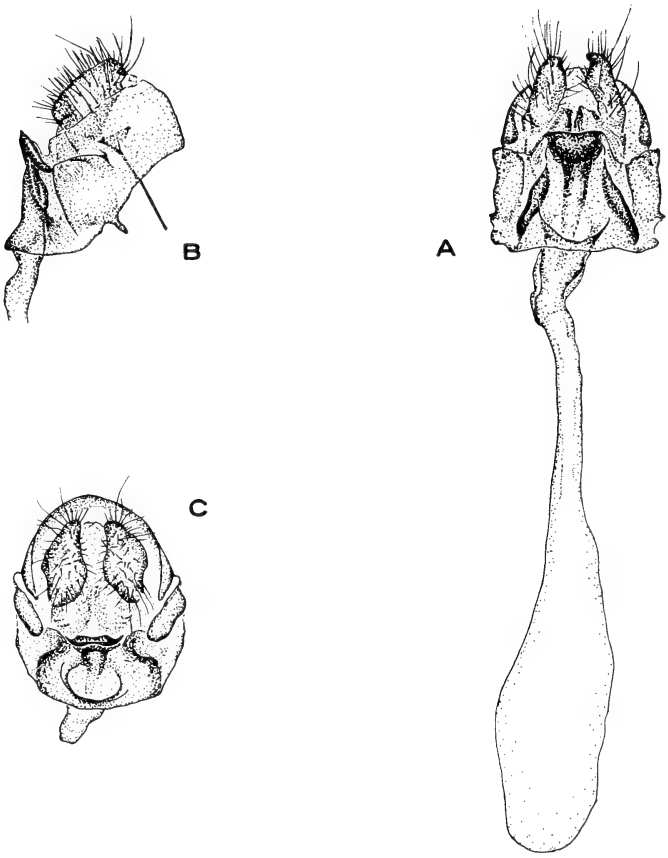

Fig. 5. Female genitalia of *Celotes nessus*. A. Ventral view of bursa copulatrix, sterigma, and ovipositor lobes. B. Right lateral view. C. Ventroposterior view. [Drawn from female from Austin, Travis County, Texas, IV-18-1967 (J. M. Burns).]

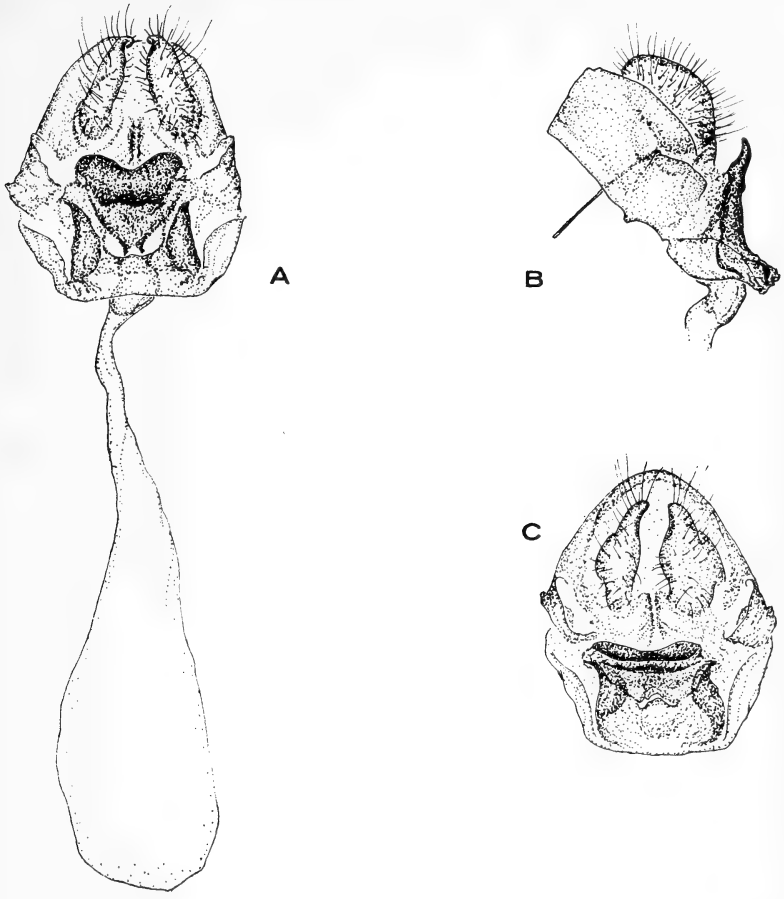

Fig. 6. Female genitalia of *Celotes limpia*. A. Ventral view of bursa copulatrix, sterigma, and ovipositor lobes. B. Left lateral view. C. Ventroposterior view. [Drawn from paratype from Limpia Canyon, 4700 feet, Davis Mountains, 5 mi. NE of Fort Davis, Jeff Davis County, Texas, V-4-1959 (J. M. and S. N. Burns).]

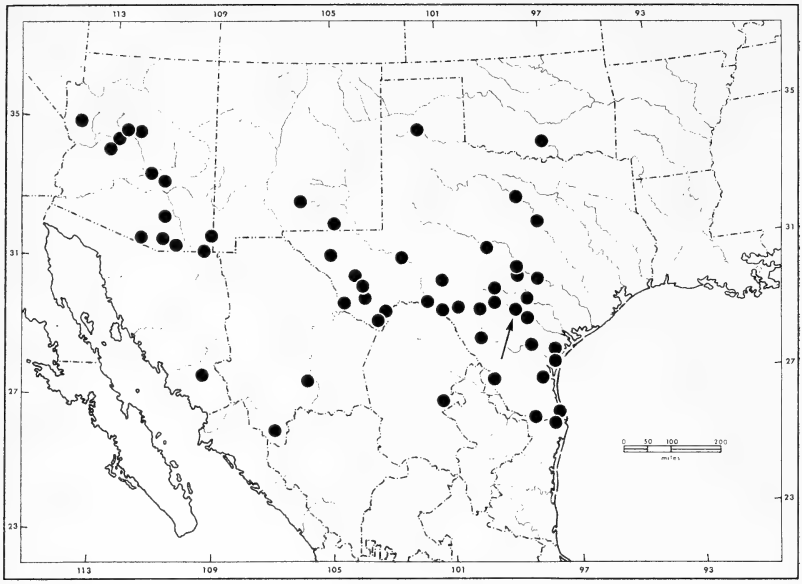

Fig. 7. Spatial distribution (based on material examined) of *Celotes nessus* — southwestern United States and northern Mexico. Rivers and the borders of states are shown. Type locality indicated by arrow.

huahua, as well as Coahuila, and, in all likelihood, beyond these states. Indeed, either *limpia* or *nessus* (see *Nomenclatural epilogue* below) was long ago reported from Durango city (Godman and Salvin 1899), and both species probably range well down the Central Plateau of Mexico. The distribution of *limpia* appears to lie *within* that of *nessus*.

Over its much broader distribution, *nessus* occurs from sea level to somewhere between 5000 and 6000 feet; *limpia,* with its strictly interior distribution, is now known from an elevational range of 1900-5700 feet. In montane regions of the southwestern United States, both skippers are species of alluvial fans, foothills, lower canyon reaches, and lower elevations generally; they avoid higher elevations.

The distribution of *nessus* in the United States is not perfectly known. The skipper may conceivably occur in the New York and Providence mountain region of southeastern California, in southern Nevada, in southern Utah, possibly in extreme southwestern or southeastern Colorado, and certainly in considerably more of New Mexico

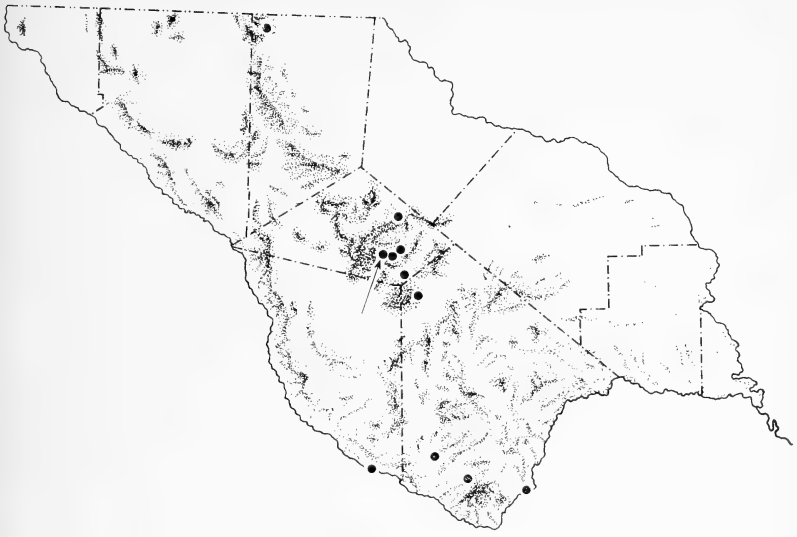

Fig. 8. Spatial distribution (based on material examined) of *Celotes limpia* — Trans-Pecos Texas. Mountains and the borders of counties are shown. Type locality indicated by arrow. The range as plotted spans a north-south distance of about 220 miles; but, since preparing this map, I have examined one male from southern Coahuila, Mexico, about 250 miles southeast of the Big Bend.

than fig. 7 indicates. On the other hand, this map probably gives a close approximation of the eastern distributional limit of *nessus*. This meridional eastern limit coincides neatly with that of many other organisms — including other pyrgine skippers of the southwestern United States and northern Mexico such as *Pyrgus philetas* Edwards (Burns and Kendall 1969) and *Erynnis meridianus* Bell (Burns 1964, and unpublished) — and reflects an important biogeographic barrier.

There are two freaky records of streaky *nessus* east of the 97th meridian. The first [Burton, Georgia, V-21-1911 (J. C. Bradley) (Cornell University collection)] was published by Harris (1950) and repeated [as "Georgia (once!)"] by Klots (1951), but was not even mentioned later by Harris (1972) and should be discounted. The second [Tallulah, Louisiana, between VIII-1926 and X-1931 (collected in the day at an altitude of 20 feet by an airplane)] was published by Glick (1939); but though it has been repeated (Lambremont 1954; Mather and Mather 1958), the feat itself has not.

Temporal distribution. — Both *limpia* and *nessus* are multivoltine, and both fly at the same times. Nearly all of the dated wild-caught adults of *Celotes* that I examined were collected from March to September: in Texas, every half-month interval from the beginning of March to mid-September includes records of both *limpia* (N = 68) and *nessus* (N = 158); however, for Arizona *nessus* (N = 183), the months of May and June together yield but 3 records, which leaves a major gap between one large cluster of records in March and April and another in July, August, and the first half of September. The only other dated wild-caught specimens examined are 5 *nessus* from far southern Arizona collected in mid-January and 5 *nessus* from the last half of September and the first half of October from central and, as might be expected, extreme southern Texas (the lower Rio Grande Valley). In the experience of Kendall (1965), *nessus* flies from early March to mid-November in Texas.

The fact that temporal distribution is essentially continuous through the warm season for both *limpia* and *nessus* in Texas but distinctly bimodal for *nessus* in Arizona probably relates to the different patterns of rainfall in the two states. For the most part, Texas has much more evenly distributed precipitation than does Arizona, where it occurs in two widely disjunct winter and summer periods. The second flight period of *nessus* in Arizona coincides with the summer rainy season, to which it is presumably geared. In the course of his field studies and laboratory rearings, Kendall (1965, and unpublished) has observed that full-grown larvae of *Celotes* are able to enter diapause (facultatively) to beat heat and drought, as well as to get through the cold of a winter season. Kendall has shown in the laboratory that such diapause can be broken by providing moisture, whereupon larvae pupate and produce adults promptly. Given this capacity to be flexible, variable larval growth rates, and the usual vicissitudes of weather, individuals of a single generation must often get out of synchrony with the result that generations overlap broadly and irregularly, forming no definite number per year in either species.

There are no indications that *limpia* and *nessus* are temporally displaced with respect to each other where they spatially coexist in Trans-Pecos Texas. Rather, my records show that adults of both species have repeatedly been collected in association — unwittingly, of course, since the collectors were unaware of the existence of more than one species of *Celotes*. On nine occasions altogether, five different collectors (or pairs of collectors) have caught a total of 37

limpia and *nessus* at the same place on exactly the same date — the places occurring in Jeff Davis and Brewster counties and the dates in March, May, June, July, and August. Many other records of both species at a single locality differ by only one to a few days.

Larval foodplants. — Numerous studies in Texas by R. O. and C. A. Kendall show that both *limpia* and *nessus* feed on various species of Malvaceae. For both skippers, the Kendalls have witnessed oviposition — directly on larval foodplants — in the wild, and have collected numerous eggs and larvae from which they have reared adults.

In the field, *limpia* eats *Abutilon malacum* Wats., *A. incanum* (Link) Sweet, *Sphaeralcea angustifolia* var. *lobata* (Woot.) Kern., and *Wissadula holosericea* (Scheele) Gke., and, in the laboratory, also *Malvastrum americanum* (L.) Torr. and *Althaea rosea* Cav. In the field, *nessus* eats *Abutilon incanum, Sphaeralcea angustifolia* var. *lobata, Wissadula holosericea, W. amplissima* (L.) R. E. Fries, and *Sida filipes* Gray, and, in the laboratory, also *Althaea rosea.* Both skippers very likely eat other mallows, as well.

Documentation: Eggs and larvae of *Celotes* were found on *Sphaeralcea angustifolia* var. *lobata* at Davis Mountains State Park, Jeff Davis County, V-1-61, by R. O. and C. A. Kendall. At the laboratory in San Antonio, those larvae that were not preserved were reared perforce on *Althaea rosea.* One adult was obtained from a larva on V-28-61 and two from eggs on VI-6 and 9-61. Although all were reported as *nessus* (Kendall 1965), I find that only the adult that emerged VI-6 is *nessus* whereas those that emerged V-28 and VI-9 are *limpia* (paratypes).

From 3 larvae found by the Kendalls on *Wissadula holosericea* in Musquiz Canyon on state highway 118, Jeff Davis County, VIII-14-66, 1 adult (a paratype of *limpia*) was obtained on IV-14-67.

From 2 larvae found by the Kendalls on *Abutilon incanum* near Rio Grande Village in Big Bend National Park, Brewster County, X-12-67, 2 adults of *limpia* (paratypes) were obtained (after a lengthy diapause) on VI-19 and 22-68. At the same locality, III-27-68, the Kendalls saw a female of *Celotes* oviposit on *A. incanum* but got only the egg and not the female; from this egg, an adult of *limpia* (paratype) was obtained on V-29-68.

The Kendalls collected 23 larvae on *Abutilon malacum,* VIII-18-66, at a point on ranch road 170 overlooking the Rio Grande, about 15 miles southeast of Redford, Presidio County; and, using *A. incanum, Malvastrum americanum,* and especially *Wissadula*

holosericea as larval food in the laboratory, they reared 22 adults of *limpia* (all paratypes) (one seemingly parasitized larva was preserved). At exactly the same spot, X-11-67, the Kendalls collected about 40 more *Celotes* larvae on *A. malacum* and reared 23 adults (apparently *limpia,* but none of them examined by me).

Foodplant records for *nessus* are legion (Kendall 1959, 1965, and unpublished). Most of them are of *Abutilon incanum;* and these come from many counties in central Texas: Bexar (innumerable records), Blanco, Bosque, Comal, Crockett, Kerr, Kimble, Llano, Maverick, McCulloch, Medina, Nueces, San Patricio, Travis, Uvalde, and Val Verde. I have examined much of the *nessus* material reared on *A. incanum.*

The one valid record of *nessus* found as an egg on *Sphaeralcea angustifolia* var. *lobata* in Jeff Davis County, Trans-Pecos Texas, and reared to an adult in the laboratory on *Althaea rosea* was discussed above; the other two adults reared from this lot of eggs and larvae on *Sphaeralcea* are actually *limpia,* though they, too, were reported (Kendall 1965) as *nessus.*

Three larvae found on *Sida filipes* in San Antonio, Bexar County, V-9-63, and kept on this plant, produced adults of *nessus* (not seen by me) on VI-8, 14, and VII-11-63 (Kendall 1965).

A larva found by the Kendalls on *Wissadula holosericea* in San Antonio, Bexar County, V-24-65, yielded an adult of *nessus* (seen by me) on VI-11-65.

Three larvae found on *W. amplissima* in extreme southern Texas at the Laguna Atascosa National Wildlife Refuge, Cameron County, IV-21-62, produced adults of *nessus* (all seen by me) on V-15, VI-4, and VIII-20-62 (Kendall 1965).

Hypodigm. — Of *limpia:* the holotype ♂ specified earlier, an allotype ♀ with identical data (except V-1-59), and paratypes comprising 64♂ 30♀ from Trans-Pecos Texas and 1♂ from Mexico. Paratypic data arranged in the system described by Burns (1964: 19-20), with names of recurring collectors abbreviated: J. M. and S. N. Burns to B, H. A. Freeman to F, and R. O. and C. A. Kendall to K.

MEXICO. Coahuila. 25 mi. N Saltillo, IX-19-69, 1♂ (J. A. Scott).

UNITED STATES. Texas. *Brewster County:* Alpine, V-20-26, 1♂ (O. C. Poling) (MCZ); V-21-26, 1♂ (O. C. Poling) (MCZ); VI-4-42, 1♂ (F); VI-5-42, 1♂ (F); VI-6-42, 3♂ (F); VI-7-49, 1♂ (F); VII-10-49, 1♀ (F); VIII-9-52, 2♂ (F); VII-28-53, 1♂ (F); VI-16-60, 1♀ (F); III-14-61, 1♂ (W. S.

McAlpine); III-27-61, 7♂ (W. S. McAlpine) (2 in PMY); VI-5-61, 1♂ (F). 8 mi. N Study Butte, 3500 ft., VII-15-63, 1♂ (H. Clench) (CM). Big Bend National Park: The Basin, 5500 ft., IV-30-65, 1♀ (K); IX-8-65, 1♂ (K). Oak Spring, 5700 ft., IX-9-65, 1♀ (K). Rio Grande Village, 1900 ft., III-27-68, 3♂ (K); V-29-68, 1♂ reared from egg (K); VI-19, 22-68, 2♂ reared from larvae (K). Window, 5500 ft., VIII-16-66, 3♂ (K). *Culberson County:* 2 mi. N Pine Springs, 5700 ft., Guadalupe Mts., VII-19-63, 6♂ (H. Clench) (CM). *Jeff Davis County:* 11 mi. N Alpine, VI-20-68, 5♂ (J. A. Scott). 13 mi. NW Alpine on state highway 118, IV-17-60, 1♂ 1♀ (K. Roever). Big Aguja Canyon, IV-2-68, 5♂ (K). Davis Mts. State Park, V-28-61, 1♂ reared from larva (K); VI-9-61, 1♀ reared from egg (K). Ft. Davis, VIII-27-54, 1♂ (R. M. Bohart). Limpia Canyon, 4800 ft., Davis Mts., 1 mi. N Ft. Davis, IV-28-59, 1♂ (B) (MCZ). Limpia Canyon, 5000 ft., Davis Mts., 4 mi. WNW Ft. Davis, IV-28-59, 2♀ (B) (MCZ); V-1-59, 2♂ 1♀ (B) (MCZ); V-2-59, 2♀ (B) (MCZ); V-4-59, 1♂ (B) (MCZ). Limpia Canyon, 4700 ft., Davis Mts., 5 mi. NE Ft. Davis, V-4-59, 1♂ 1♀ (B) (MCZ). Musquiz Canyon on state highway 118, VIII-14-66, 2♂ (K); IV-14-67, 1♀ reared from larva (K). *Presidio County:* 30 mi. SE Presidio along Rio Grande, III-26-66, 2♀ (D. J. Lennox). 15 mi. SE Redford on ranch road 170, 2500 ft., VIII-29, 30, 31-66 and IX-1, 4, 5, 6, 7, 8, 9, 10, 11, 17, 29-66, 7♂ 15♀ reared from larvae (K).

Hypodigm of *nessus* summarized in table 2.

Table 2. Specimens of *Celotes nessus* examined.

COUNTRY State	♂	♀	N
MEXICO			
Chihuahua	3	1	4
Coahuila		2	2
Sonora	7		7
UNITED STATES			
Arizona	169	24	193
New Mexico	8	2	10
Oklahoma	1	1	2
Texas	147	67	214
N =	335	97	432

Nomenclatural epilogue. — A species of what we now call *Celotes* was named three times within less than a decade, 1877 to 1884 (see e.g. Lindsey, Bell and Williams 1931; Evans 1953). In order of publication, the names are *Pholisora nessus* Edwards, *Spilothyrus notabilis* Strecker, and *Carcharodus radiatus* Plötz. The fact that I have made no effort to examine types is not so cavalier as it might seem. On the one hand, genus *Celotes* is such a distinctive element of the American fauna that one may safely assume that all three names have long since been assigned to it correctly. On the other hand, one may also assume that all three refer to *nessus* rather than to *limpia* for the following reasons. The type locality for both *nessus* and *notabilis* is San Antonio (or perhaps the nearby town of New Braunfels for the latter), at the eastern edge of the main range of *nessus* and therefore a few hundred miles removed from the nearest populations of *limpia* in Trans-Pecos Texas. Because intervening areas have now been well-collected, the total lack of *limpia* from eastcentral Texas is real. The type locality for *radiatus* is simply Texas; but, inasmuch as the name was published in 1884, the material on which it was based almost certainly came from central Texas, too. The west Texas areas in which *limpia* occurs are relatively remote. Indeed, in all of the material assembled from museums for this study, there were only two specimens of *limpia* that had been collected prior to 1961 — and they were taken in 1926.

Godman and Salvin (1899) proposed *Celotes* as a monotypic genus with *Pholisora nessus* Edwards as its type-species. There is some historical and distributional interest in noting that their hypodigm of *"nessus"* undoubtedly included *nessus* but may have been mixed. As they themselves said, it comprised 3 specimens from Texas provided by Strecker and 3 from Mexico (Northern Sonora and Durango city). Strecker's *notabilis* (=*nessus*) was one of a series of lepidopterans that he described from material collected "by Mr. J. Boll, mostly in the vicinity of New Braunfels and San Antonia [sic]" (Strecker 1878). Owing to its geographic origin, the Strecker material certainly — and that from Northern Sonora almost certainly — would have been *nessus*. Furthermore, the male genitalia that Godman and Salvin clearly figured (pl. 91, fig. 29) belong without question to *nessus*. The Durango material is problematic, however. To judge from the locality, it might almost as well be *limpia* as *nessus*. Godman and Salvin's color illustrations of dorsal and ventral aspects of a female of *Celotes* (pl. 91, figs. 27, 28) could be taken for either species, the dorsal view (fig. 27), in particular, being

rather more reminiscent of *limpia* with respect to both facies and size. Unfortunately, the geographic source(s) of the female(s) on which these figures are based was not indicated, but probability favors Mexico: Evans (1953) records that the holdings of the British Museum by then included 10 specimens of *nessus* from Texas, of which just 2 are females, but still only 3 from Mexico, to wit, "1 ♂ 2♀" from "N. Sonora. Durango." I would not be surprised to find that Godman and Salvin depicted a female of *limpia* from Durango.

Summary

Celotes limpia, a new species of skipper butterfly in a hitherto monotypic genus, is described and extensively compared with *C. nessus,* which it closely resembles in superficial appearance and biology. Of 529 specimens examined, 97 represent the new species. Whereas *C. nessus* ranges widely (from central Texas and Oklahoma west to northwestern Arizona and south to at least the northern tier of Mexican states), *C. limpia* is relatively restricted, occurring within the range of *C. nessus* in Trans-Pecos Texas and interior northern Mexico. In Trans-Pecos Texas, where the only direct comparisons could be made, the two species are not only sympatric but also synchronic, flying in an indefinite number of generations from March to September. Larvae of both skippers are known, in the field, to eat various plants in the Malvaceae: *Abutilon incanum, A. malacum* (*limpia* only), *Wissadula holosericea, W. amplissima* (*nessus* only), *Sphaeralcea angustifolia* var. *lobata,* and *Sida filipes* (*nessus* only). In the laboratory, additional malvaceous foodplants are *Althaea rosea* and *Malvastrum americanum* (*limpia* only). *Celotes limpia* and *C. nessus* differ slightly in size and strikingly in genitalic morphology (both male and female) and in the morphology of certain scales on a male secondary sex character having a presumed communicative function.

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A REMARKABLE NEW ISLAND ISOLATE IN THE ANT GENUS *PROCERATIUM* (HYMENOPTERA: FORMICIDAE)

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In 1969, I collected in southern Africa and Madagascar, and then moved on for work in southern India, stopping en route for four days (29 March-1 April) on Mauritius in order to sample the small but interesting endemic ant fauna known from this island in the Indian Ocean. My experience there was greatly enriched by aid and information from Mr. Leo Edgerly, retired chief forester of Mauritius, whose knowledge of the island and its plants, animals and people is probably unmatched.

On the second day of my stay, on Mr. Edgerly's advice, I climbed the small mountain known as Le Pouce ("The Thumb") in the Moka Range in the northern part of the island. This mountain, formerly collected by the Mauritian entomologists R. Mamet and J. Vinson, is described in Donisthorpe's paper (1946) on the ants of Mauritius. The Moka Range rises from a sea of sugar cane, and Le Pouce is separated from neighboring mountains in the narrow volcanic chain by deep saddles. It is an elongate massif, with tall, steeply dropping cliffs on all sides and a topside "plateau" sloping up gently eastward to a sudden sharp peak that gives the mountain its name. The plateau averages about 700 m in elevation; it is still largely covered with a low, gnarled native forest much invaded by guava and grassland. A mostly gentle trail hugs the cliffs and crosses the plateau.

The first day on Le Pouce was a bright, sunny Sunday, and the few well-marked trails through the pleateau scrub were invaded by bands of teenagers from the lowlands, equipped with portable radios. Accordingly, I stuck to the heavy vegetation. Ants were very scarce, and nearly all that I found were colonies of the small dark *Solenop-*

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sis mameti in rotten wood. Near the end of the day, when the sun was getting low, I was at the eastern end of the plateau where it begins to rise suddenly to the peak. Here a 2-centimeter-thick hollow rotting stick lying on the leaf litter unexpectedly yielded a nest of sluggish red ponerines, obviously Ectatommini in habitus. I got the nest alive into a plastic "live tube" and kept it for a week until it succumbed to mold. I was much excited by the find, although I assumed at the time that I had a species of *Gnamptogenys* belonging to the Indo-Australian *"Stictoponera"* group, because of the rather large size and more or less shining integument of the workers, and the distinct (though small to a hand lens) eyes. Even this would have been a remarkable range extension.

On the next day I collected in other parts of the island, including the scrubby "peat forest" on high ground in the south, then being destroyed and replanted (disastrously!) with hurricane-vulnerable exotic pines. The bag was discouraging, consisting almost entirely of introduced ant species. A rapid traverse with Mr. Edgerly of the southern Cocotte Mountain, badly stripped by a recent hurricane, turned up nothing but introduced ants.

On the first of April, though I was scheduled to leave on an eveing flight to Bombay, I tried Le Pouce again. A telephone call to Mr. J. Vinson, who had collected some of Donisthorpe's material, convinced me that the main path on the LePouce plateau should not be avoided. I arrived there early in the afternoon; the day was heavily overcast, threatening rain on the peaks, and it took me about an hour to walk up to the plateau. Whereas the sunny Sunday in the scrub shade had yielded almost no ants foraging, I now found foragers on foliage and on the hard-packed earth of the trail every few meters of the way.

These were mostly *Camponotus aurosus* and *Pristomyrmex* spp. (=*Dodous*), native Mauritian species. Before long, on the trunk of a small tree by the path, I found a sparse trail of bright red ants climbing the bark. Closer examination revealed these to be predominantly the ectatommine I had collected on the previous Sunday, but interspersed with these were workers of *Pristomyrmex bispinosus* (Brown, 1971) which, with their gasters carried partly curled under, looked remarkably like the ectatommines. It is hard to avoid the impression that some kind of mimicry involves these two species in this habitat. The ectatommines ascending the trunk nearly all carried in their mandibles tiny whitish spherical objects that proved eventually to be arthropod eggs — probably spider eggs.

I climbed the tree, which was only about 5 meters high, and soon found the nest about 3 meters up. Where two of the gnarled branches crossed, a thick pad of lichens surrounded the place where they touched. Forcing the branches apart, I found a rotted-out pocket, evidently caused by their rubbing together in high winds. The cavity extended downward several centimeters into one of the branches, and it was full of the ectatommine ants with brood and many of the round white arthropod eggs; I estimate that I removed or saw at least 200 workers, and there may have been more. The nest was very inconveniently placed, and the branch was too thick to break or cut with the small knife I had along, so I had to be satisfied with what I could extract by means of a twig wetted with alcohol, and with my fingers and forceps.

A few minutes later along the trail, I found the entrance to another nest in a small tree, also about 3 m above ground, and like the first one of that day, also in a rot hole covered with lichens. I took a few workers from near the entrance, and later found two foraging workers on the hard-packed earth of the trail. Further observations were made impossible by a sudden torrential rain, and it was only with great difficulty that I got back down off the mountain, partially dried out my clothes, and reached the airport in time for the flight to India.

My hosts in Calicut, Drs. A. Benedict Soans and Joyce Soans, gave me access to a stereomicroscope, and I quickly learned that the ectatommines I had were not *Gnamptogenys,* but *Proceratium!* I offer a formal description of the new *Proceratium* species, followed by a discussion of its relationships and its evolutionary and zoogeographic significance.

Proceratium avium new species

Figs. 1, 2

Holotype worker: TL 4.8, HL 0.96, HW 0.94 (CI 98), ML 0.32, scape L 0.93, greatest diameter of eye 0.09, WL 1.43, L petiole in side view 0.60, L petiolar node as seen from above 0.47, W petiolar node 0.47, L hind tibia 0.97, L hind metatarsus 0.81 mm. For head length (HL), measurement is taken from the anterior lateral corners of the head (clypeus); head width (HW) excludes the eyes, and is taken just behind them. The petiolar node length excludes the brief anterior peduncle and is taken from the approximate base of the anterior nodal slope. The length of the gaster is

taken in side view from the dorsal side of the juncture with the postpetiole straight to the most posterior part of the curve of the second (downcurved) gastric segment (true abdominal segment IV).

Paratype workers (19 measured from 3 colonies at the type locality): TL 4.7-5.0, HL 0.92-0.98, HW 0.91-0.98 (CI 96-101), ML 0.31-0.34, scape L 0.90-0.99, greatest diameter of eye close to 0.09, WL 1.38-1.49, L petiole in side view 0.59-0.61, L petiolar node 0.42-0.47, W petiolar node 0.41-0.47, L hind tibia 0.96-1.02, L hind metatarsus 0.80-0.87 mm.

Composite description: Form of head and body more or less as shown in Figs. 1 and 2. Variation occurs in the following traits: Posterior border of head in full-face view varying from transverse, nearly straight (holotype) to broadly rounded with or without a narrow flattened or even feebly concave median portion, as in Fig. 2. Nuchal carina (on cervical face of head) continuing as a ventrolateral margin halfway down each side of head. Sides of head varying from approximately straight and parallel (Fig. 2) to gently convex and slightly converging anteriad. Eyes each composed of a single clear, convex facet. Median lobe of clypeus with sides feebly sinuous, as in Fig. 2, or merely weakly convex. Mandibles with 4 strong teeth, but one of these is sometimes double; in addition a small offset tooth is sometimes developed at the basal angle, normally hidden when closure is complete. The inner margin of the peduncle of the mandible has a low, suboblong, sinuous or even bidentate ridge or lamella, visible only when the mandible is open. The scapes vary in length and slightly in apical thickness, so that when laid straight back they surpass the posterior border of the head by amounts ranging from less than half their apical thickness to more than their apical thickness.

Labral shield bilobate, the lobes separated by a broad V-shaped notch; also, lateral to each lobe is a small thumb-shaped lobe or knob extending dorsomesally (flexad) of the plane of the shield from its basal ridge. Maxillary palpi 4-segmented, the basal segment short and cylindrical, the second segment flat and attached to the basal segment at nearly a right angle by a peduncle that arises from the side of II; III and IV are short elliptical segments extending in line from II. This is the characteristic form of maxillary palpi in *Proceratium*. Labial palpi 3-segmented.

Trunk convex from side to side, and from front to rear in side view, but the portion of the outline from mesonotum to propodeal declivity may be straight or may be interrupted by a feeble dip or saddle in the region of the obsolete metanotal groove. The propodeal

angles may be smoothly rounded, as in Fig. 2, or may bear very low, obtuse corners that also render the sides of the declivity vaguely submarginate (30 March colony) as opposed to the rounded sides of the declivity in the 1 April series (Fig. 2), taken less than half a kilometer away. Seen from above, trunk broadly rounded in front, sutureless, tapering gently caudad, with a feeble suggestion of constriction behind mesonotum.

Petiole briefly pedunculate in front, the peduncle with strong anterolateral cornuae, the node varying from loaf-shaped with relatively steep, rounded anterior face (Fig. 2) and rounded sides to a lower version with more gradually sloping anterior face and sides less bulging. Postpetiolar (first gastric) segment varying in dorsoventral depth, especially near the posterior quarter or third of its length, and the individuals with deeper postpetiole tend to have the tergum of this sgment more swollen (or humped as seen in side view) than in the paratype depicted in Fig. 2.

Integument overall smooth and decidedly shining, but head, trunk, node and postpetiolar (first gastric) segment thickly sown with circular, centrally-tuberculate and piligerous foveae or coarse punctures. These foveae tend to be larger and more densely arranged, even subcontiguous in places (e.g., in the region behind the eyes), in the 30 March colony as compared with the series of 1 April, but the latter series vary greatly in this respect, even within samples from the same nest. The least strongly punctured individuals have the dorsa of trunk, node and postpetiole almost completely smooth and shining, the punctures here small and sparse. Antennae and legs much more finely and densely punctate, becoming more opaque apicad. Median clypeal lobe finely punctate-rugulose in a longitudinal direction; mandibles striate-punctate, but shining and coarsely punctate toward apicolateral margins. Second gastric (IV true abdominal) segment smooth, shining, with sparse piligerous punctulae. Gastric apex finely and densely punctulate, subopaque.

Pilosity abundant, moderate and uneven in length, of fine, subdecumbent to suberect tapered hairs, a little longer but much less abundant than usual in *Proceratium,* grading into a much shorter, appressed to decumbent pubescence-like covering as one moves apicad on antennae, legs and toward gastric apex; also a fine, appressed, medially-directed pubescence in the space between eyes and frontal carinae.

Color (of fully mature individuals) rich bright ferruginous red, legs and scapes often lighter and more yellowish; region immediately

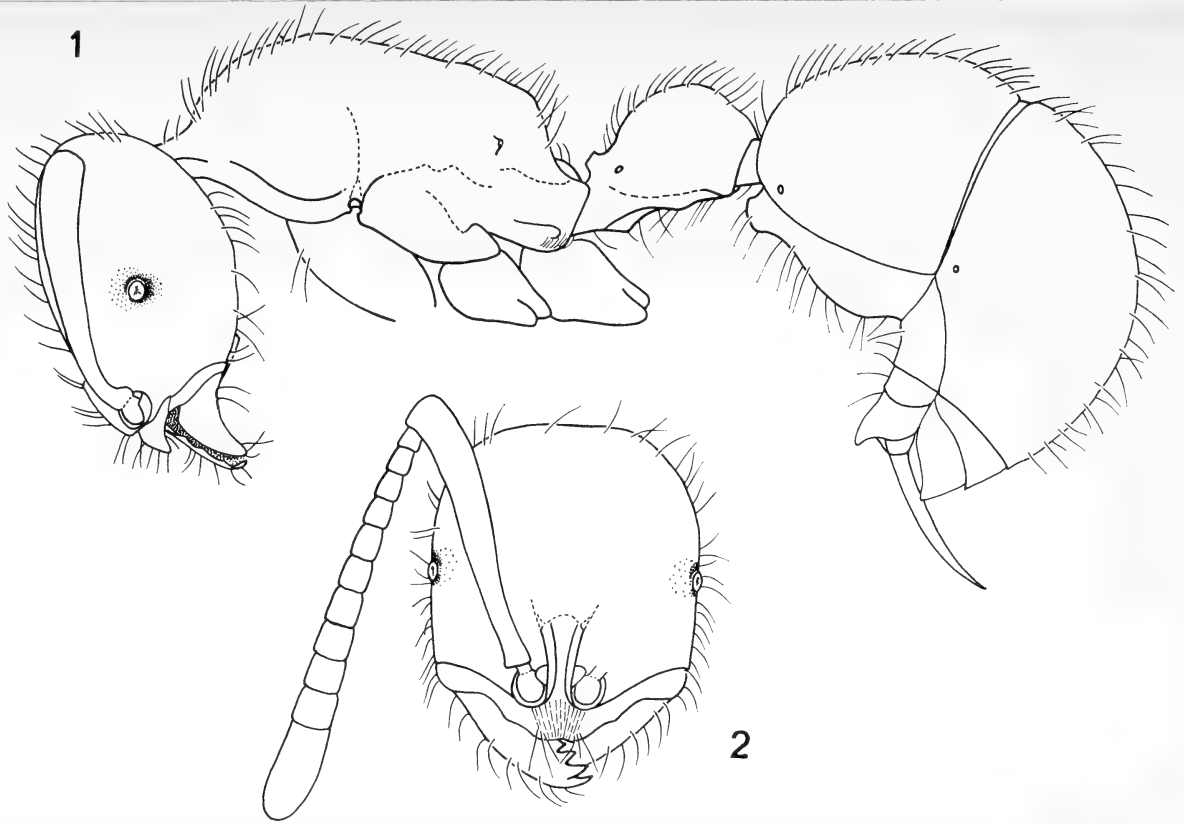

Fig. 1. *Proceratium avium* new species, paratype worker in side view; only the longer hairs seen in silhouette are shown (from colony No. M-252, 1 April 1969).

Fig. 2. Same, full-face view of head. Drawings by Bente King.

around eyes often with darker pigment. Some specimens, presumably nearer to being callow, are lighter, more yellowish-ferruginous in general color.

Malpighian tubules numbered 6 each in 4 live workers dissected, and 4 in a fifth worker, the last probably representing a mutilated specimen (dissected under less than ideal conditions). Not cryptonephric. The count of 6 agrees with a worker of *P. goliath* dissected in Costa Rica.

Queen, subergatoid (from 30 March colony): TL 5.1, HL 0.90, HW 0.92 (CI 102), ML 0.34 (mandibles slightly opened), scape L 0.83, greatest diameter of eye 0.14, WL 1.38, petiole L (from above) 0.57, petiole W. 0.58, L hind tibia 0.87, L hind metatarsus 0.71 mm. Head as in worker, of the shape with transverse, only feebly convex posterior border in full-face view; sides converging slightly from behind eyes toward mandibles, and bulging again slightly at lateral ends of clypeus. Mandibles with 5 moderately strong teeth and a small offset basal tooth. Ocelli small but distinct; compound eyes nearly circular in outline, moderately convex, with an estimated 70 distinct ommatidia, relatively smaller than usual in *Proceratium* queens. Scapes just barely overreaching posterior border of head when laid straight back.

Trunk somewhat reduced, but the usual sclerites of the pterothorax separated, except that the elements of the mesonotum are all indistinguishably fused into one gently convex continuous shield; metanotum distinct but narrow, forming the usual acute median process, but in short compressed form. Propodeum with slightly raised, but bluntly rounded angles and slightly concave, submargined declivity. Wing stumps present and blackened, but small.

Petiole shorter, broader and a little higher than in worker, the node rounded above and with a rather steep anterior face. Gaster much deeper and broader than in worker, extraordinarily voluminous, but undercurved as in worker. Sting present, stout, protrusible.

Sculpture, color and pilosity much as in the worker over head, trunk and petiole, but the punctures here shallower, less distinct and sparser than in even the more weakly foveate workers; mesonotum and node with obsolescent foveae, almost completely smooth, shining. Gaster smooth and shining, without coarse punctures, but very finely and densely punctulate, with associated dense, short, appressed pubescence and a few short, delicate decumbent to erect hairs, mainly at the posterior borders of the first segment and on the undersurfaces, and becoming abundant near the gastric apex. Due to the great bulk

of the gaster, the fusion of the mesonotal sclerites, and the small eyes, I doubt if this queen ever had flight-functional wings.

Male (from 30 March colony): TL 4.7, HL 0.76, HW (including eyes) 0.98, ML 0.29, scape L 0.64, greatest diameter of compound eye 0.40, WL 1.55, L petiole 0.55, W petiole 0.35, L hind tibia 0.93, L hind metatarsus 0.80, forewing 4.0 mm.

Head with high-domed vertex set with 3 large, clear ocelli; compound eyes large and strongly bulging, with convex inner margins as seen in full-face view of head. Median lobe of clypeus projecting, broadly truncate. Frontal carinae parallel, low but sharp, vertically raised. Mandibles triangular, each ending in a stout curved apical tooth, masticatory borders curved and cultrate. Scapes overreaching posterior border of vertex. Palpi segmented, as far as can be seen in the undissected specimen, as in worker.

Alitrunk with well-developed flight sclerites and wings; notauli lacking; scutellum semiglobose, protruding. Metanotum with the usual stout, acute median tooth. Propodeal dorsum short, convex, rounding obtusely into the declivity, which is indistinctly marginate on the sides.

Petiole long and very low, with the highest part of the gently convex node near midlength, but the greatest width at about the posterior third. Postpetiole anteriorly wider than petiole, and widening still more posteriad, but not quite as wide as the succeeding segment, which is vaulted ventrad, but not as strongly as in worker and queen.

Genitalia largely retracted (not dissected), but it can be seen that the parameres have thin, broadly rounded apices that are bent mesad toward each other.

Legs long and slender, with the usual single pectinate spur on each middle and hind tibial apex, and the tarsal claw slender and simple.

Wings of basic *Proceratium* pattern, with Rsf2-3 completely lacking in the forewing; m-cu also gone; the enlarged "cubital" cell receives only one free vein distally (Rsf5), because the apical free abscissa of M is gone. In the hind wing, the large cell receives a short remnant of Rs and the longer free apical abscissae of M and CuA; 1A is missing beyond cu-a. Wings hyaline, with light brown veins. (In the newly-discovered males of the related *P. stictum* — from Brookvale, Queensland, and *P. goliath* — from Zent, Costa Rica, the venation pattern is similar to that of *avium,* but darker in *goliath,* still paler in *stictum;* m-cu is preserved in *stictum,* but in the hindwings of both, the free abscissa of Rs is reduced to obsolescence.)

Sculpture shining, with foveae much as in the worker, but also with rugulae and more opaque around the eyes, posterior scutellum, dorsum and sides of propodeum, metanotum and sides of petiole. Pilosity fine, rather short, moderately abundant, decumbent to suberect, generally distributed over body, scapes and legs. Color light yellowish-brown, gaster more brownish; vertex infuscated near ocelli and in back of compound eyes.

Holotype (from unnumbered colony, 1 April 1969) and paratypes (colonies ICA-69, 30 March 1969; M-252 and an unnumbered colony, plus strays, 1 April 1969) taken from Le Pouce (mountain), Mauritius, in native forest between 700 and 800 meters elevation on the plateau just below the peak (W. L. Brown, Jr.). Holotype and paratypes deposited in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. Paratypes in Cornell University Collection, British Museum (Natural History), Australian National Insect Collection, Canberra, Australia, and elsewhere.

P. avium belongs to the *stictum* group of *Proceratium,* containing two other species. *P. stictum* (Brown, 1958;366) has been known only from a single worker from North Queensland. (Now I have seen males apparently belonging to *stictum,* taken at light by E. S. Ross and D. Q. Cavagnaro at Brookvale, Queensland; and R. W. Taylor showed me a series that I was only able to examine hurriedly, but which looked to me like *stictum,* from his collections made in North Borneo.) The second species of the *stictum* group is *P. goliath* (Kempf and Brown, 1968:94 ff.) from Costa Rica. *P. avium* is distinct from both of these species in its much shinier and coarser sculpture and in details of the shape of the trunk, particularly its completely unarmed propodeum, in its longer antennae, and in its less strongly undercurved gaster. *P. avium* is also much larger than *P. stictum,* but smaller than *P. goliath,* and its eyes are relatively larger than in either of these species. In fact, *P. avium* might well go into a group of its own, but the structure of the clypeus, mandibles, and petiole are so much like those of *P. stictum* and *P. goliath* that the relationship of these three species is obvious.

The characters they share are also primitive for the genus *Proceratium,* and this with the widely discontinuous known distribution of the group suggests that the *stictum* group represents the relicts of an early dispersal wave of a primitive *Proceratium* stock that spread widely over the earth and was overtaken (except on Mauritius) by later waves of more advanced *Proceratium* groups. Possibly wide-

spread extinction of *stictum*-group stocks ensued; although it is not easy to visualize significant competition among such rarely-collected species, I should point out that the adaptive zone (predation of spider eggs) is a limited one. Furthermore, advanced methods of collecting, at least in North America, have proven that some advanced *Proceratium* species are common in suitable microhabitats. These microhabitats are, so far as we can tell, all cryptic ones — above all, in large masses of well-rotted wood. This may, of course, be an artifact of biased collecting methods, but I doubt it. On the northern fringes of the range of *Proceratium* — for example, in the environs of Boston — *P. silaceum* and *P. pergandei* are taken occasionally, but always under rocks in the soil. Farther south in the U.S., almost all collections are made deep in rotten wood or in humus and litter near rotten wood. The type series of *P. goliath* came from a rotten log in wet tropical forest.

The microhabitat of *P. avium,* to judge from the limited observations I have made, differs strikingly from that of other *Proceratium*. Certainly, the nest site is different. The first nest of *P. avium* taken on Mauritius came, it is true, from a hollow rotting stick lying on the forest floor. This may be a common kind of site for the species, yet very many such branchlets were examined on the day of collection without success, and it is possible that the branchlet had fallen recently from a tree above. In any case, I have never seen any of the eight other *Proceratium* species collected alive by myself in various countries nesting in such a large cavity in such an exposed site as was the colony in this stick. The other two *P. avium* nests seen were of course arboreal, with the foraging trails openly exposed for some meters over open soil and tree trunk. The ground and arboreal nesting sites for ants in wet tropical montane forest are rather academically distinguished in any case, but it seems to me that the *exposure* of the nests and foraging trails of *P. avium* is what is significant here. If other species of *Proceratium* forage so openly day or night, it has not been noted as far as I know, and indications are against it.

Of greatest interest is the contrast in habitus, especially that part owing to sculpture and pilosity, between *P. avium* and its congeners. In *P. avium,* the looser, coarser, more shining integument and its fairly long open pilosity may be compared with the finely rugulose-punctate or reticulopunctulate sculpture and very short, fine, more or less dense pilosity of the other *Proceratium* species. There is every reason to believe that these fine, crowded punctures and their associated hairs are a specialized evolutionary development (pushed further

in *Discothyrea*) stemming from a condition in which the integument was more coarsely sculptured, with larger foveae, each fovea bearing a hair on a central tubercle. The Old World (Indo-Melanesian) *Gnamptogenys* stocks include species (e.g., *G. menadensis*) that meet these specifications and are known to be epigaeic, even arboreal, foragers (personal observations), but *Gnamptogenys* has reduced palpal segmentation and other characters that make it more likely a convergent than an ancestral stock to *Proceratium*.

I believe that *Acanthoponera* is nearer to the ancestral line of *Proceratium* because of the higher basic palpal segment number and the traces in some *Proceratium* species of a median carina on the frontal area and vertex of the head, characters of *Acanthoponera* (Brown, 1958:188). But the main question we are led to consider is: Has *P. avium* preserved some version of the archetypal *Proceratium* sculpture-pilosity pattern, or is its present condition a secondary reversion from the fine-scale pattern characteristic of other *Proceratium* around the world?

Possibly we shall never have a clearly definitive answer to this question, but we do have one clue pointing toward the reversion hypothesis. This clue is the rather unusual eyes of *P. avium* — a rather large, glassy-looking orb on each side, backed by a perceptible amount of dark pigment, and relatively larger than the characteristically single-facetted "compound" eyes of other *Proceratium* species. I think we have to suppose that the ancestors of *P. avium,* and also of all other *Proceratium,* had already specialized for a cryptic existence to the point where minute single-facetted eyes, probably barely enough to sense the difference between light and dark, served adequately the lifeways of these animals. My guess is that such lifeways also had forced selection for the fine sculpture-pilosity pattern of *Proceratium* in the ancestral lineage of this genus. If my reasoning is correct, then *P. avium* is an interesting example of a "character-released" species on a remote oceanic island with a depauperate endemic ant fauna.

The known endemic ant fauna of *Mauritius* numbers only about 7 species, if we take Donisthorpe's (1946, 1949) count as a base and deduct obviously introduced species, including synonyms, and add my collections. The endemics now appear to be restricted to the small areas of upland native forest; the cane fields and other culture areas are saturated with introduced ant species. In a sense, then, the mountain forests represent the "real" island(s) of Mauritius as far as the endemics are concerned.

Among the ants of the present endemic fauna, it is difficult to pick out any that might be serious competitors of *Proceratium avium.* Our assumption here, of course, is that *P. avium* subsists primarily on arthropod eggs, probably mainly the eggs of spiders. (But the assumption rests on only a few observations, which need augmentation.). Perhaps *Solenopsis mameti,* a much smaller ant that nests mainly in rotten wood in forest shade, would qualify as a competitor. This judgement is based on the generalized feeding habits of similar-sized *Solenopsis* elsewhere in the world, and we have absolutely no direct information on the food of *S. mameti.* At least, the species has not been seen foraging on open paths or tree trunks during the day.

The bright red color and open-trail foraging of *P. avium* suggests reduced predation pressure in the Mauritian native forest habitat, but the possible mimicry with *Pristomyrmex bispinosus* could on the other hand indicate that predator pressure is appreciable, and in some way answered by protective properties.

In summary, a reasonable hyothesis to explain the atypical "epigaeic characters" of *P. avium* assumes that the ancestral stock reached Mauritius a long time ago from Africa or Asia in a floating log or rotting branch, and established itself in an ant-poor environment that was perhaps also weak in the kinds of predators that attack open-foraging ants. Evolution in such an environment, it is argued, led to the reacquisition of characters that had been lost by the parent *Proceratium* stock during continental specialization to cryptic environments in which arthropod (spider?) eggs had become its main food.

Another hypothesis is that the Mauritian *Proceratium* retains a sculptural-pilosity pattern primitive for the genus, and that its arthropod egg-feeding proclivities were acquired in an open-foraging situation that elsewhere has since been modified under continental pressures of competition and predation.

In order to throw light on the question, it would be interesting to know exactly what animals the prey eggs on Mauritius belong to, and where and how they are taken by the ants. It may be that we shall never find out, for the mountain forests of Mauritius appear to be teetering on the brink of extinction.

Notes on other species of *Proceratium*

Since my summary of *Proceratium* (Brown, 1958: 241-248), the genus has been found in additional parts of the world. Leston

(1971, J. Entomol. (B) 40: 118-119, figs. 1, 2, worker, queen) described *P. boltoni* from Ghana; this species appears to be a fourth member of the *stictum* group, perhaps annectant to the *pergandei* group.

Borgmeier (1959, An. Acad. Brasil. Ci., 31: 309, worker) described *P. brasiliense,* a close relative of the Central American-Mexican *P. micrommatum,* from southeastern Brasil; it is the first representative of the genus from so far south in the New World.

I have found a lone *Proceratium* queen in rotten wood in wet forest on the lower slopes of Mt. Klabat in northeastern Celebes. The specimen is in the *silaceum* group and is fairly near *P. carinifrons* and *P. lombokense.*

Roy Snelling has published a paper (1967, Contrib. Sci. Los Angeles County Mus., 124: 1-10.) giving further data on *P. californicum* of the West Coast of the United States, plus a key to the New World *Proceratium* species. The species of the *micrommatum* group are, however, very close to one another, and I suspect that *P. convexiceps* may eventually be shown to be synonymous with *P. micrommatum,* because the chief character — presence or absence of a triangular median lobe or tooth on the clypeus — involves this small tooth that is very variable in size in the samples from Panama and Mexico. *P. micrommatum* seems to be widespread in Mexico: Chichicastle, Tabasco (F. Bonet); Pueblo Nuevo, Veracruz (E. O. Wilson); Mesa de Chipinque, near Monterrey, Nuevo Leon (S. and J. Peck); Antiguo Morelos, Tamaulipas, litter of palm-thorn forest (S. and J. Peck).

P. normandi Santschi (1929, Bull. Soc. Ent. Belg., 69: 138, worker, queen; type locality La Caille, Algeria and Ain Draham, Tunisia) is a **new synonym** of *P. numidicum* Santschi (1912, Bull. Soc. Hist. Nat. Afr. Nord, 4: 172-173, figs. 1, 2, worker, queen; type locality Ain Draham, Tunisia). In the Santschi Collection, Naturhistorisches Museum, Basel, the types of *P. numidicum* are callow in part, but I could find no other differences between them and the types of *P. normandi* in the same collection.

Proceratium mancum Mann (1922, Proc. U. S. Nat. Mus., 61 (13): 6-7, worker, queen; type locality: Cecilia, Honduras) is a **new synonym** of *P. silaceum* Roger (1863, Berlin. Entomol. Zeitschr., 7: 172, worker; type locality "Nord-America"). The differences cited by Mann and listed in Snelling's key are all very variable in *P. silaceum,* as is body size. Specimens from the tropical part of the range usually have the petiolar node thinner from front

to rear, and the posterior face is more or less concave and overhung by the slightly produced posterodorsal nodal border, but a tendency in this direction is seen in some northern specimens, for instance, in a worker from the Ouachita Mts. of southwestern Arkansas, and one from Schooler Lake, Choctaw Co., Oklahoma (W. L. Brown). The geographical gap between Honduras and eastern U. S. is now being filled in to some extent. Already in 1911, W. M. Wheeler had collected specimens in Guatemala (Quirigua and without locality except for the country), and now S. and J. Peck have sent samples from litter berlesates in Veracruz, Mexico: near Cordoba, and in the canyon of the Rio Metlac, near Fortin de las Flores. It should only be a matter of time until we have samples from east Texas and Tamaulipas. This case is paralleled by that of *Cryptopone gilva,* another ponerine that ranges from the U. S. down through the uplands of Mexico and Central America as far as Panama.

P. goliath was taken at Zent, Costa Rica by N. A. Weber, the collection being the first male known for the species, date 17 July 1956. A worker apparently belonging to this species, but a little smaller than the types from Costa Rica, and with a very deep constriction between postpetiole and succeeding segment, comes from Caves Branch, British Honduras (berlesate, S. and J. Peck).

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SEXUAL BIOLOGY, CHROMOSOMES, DEVELOPMENT, LIFE HISTORIES AND PARASITES OF *BOREUS*, ESPECIALLY OF *B. NOTOPERATES*. A SOUTHERN CALIFORNIA *BOREUS*. II. (MECOPTERA: BOREIDAE)*

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Introduction

This, the second of three accounts devoted primarily to *Boreus notoperates* Cooper, deals with aspects of its life history. The subjects include, among others, sex ratio, mating, developmental stages, a brief comparative account of its cytology, its host mosses and peculiar adaptation to a life in their thin sods on diorite boulders in a region annually subject to long periods of drought and considerable heat. All of this is placed in a framework of what is now known for the other species of *Boreus* on these topics.

Though some fifty or so articles are referred to or discussed that are devoted to, or comment upon, *Boreus,* there are an additional sixty to seventy more papers and accounts which, though all have been consulted, either do not bear directly on the topics treated, or seem wholly derivative. My choice of references is based upon their substantial treatment of a subject, their content of new observations or ideas, or the need to correct a standing error. To these sources, I have added my own unpublished observations on *B. brumalis* Fitch and *B. nivoriundus* Fitch where relevant. The overall aim, then, is to draw together, to compare, and, where possible, to generalize what is known of the species of *Boreus* on the topics presented and on which I have information derived from *B. notoperates.*

Among the matters given emphasis are: the likelihood that species of *Boreus* have a sex ratio approaching equality (a debated topic); the fact that *B. notoperates* is the only species (of eight for which information is known) that deviates in its mating; the curious reciprocal intromission at mating by male and female alike, and the anatomical relations of their parts; the conservative nature of the chromosomal cytology of *Boreus* and other scorpion flies as compared with *Panorpa;* the prevalence of a larval epistomal suture, which

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bears upon the tenability of the order Neomecoptera that specially sets *Boreus* apart from other scorpion flies; the likelihood that *Boreus,* like other Mecoptera, has four larval instars; the occurrence of both pupal and adult pharate stages in development; that whatever limits the distribution of a species of *Boreus,* it is *not* its host mosses; and finally, that *Boreus* species, despite their peculiar life cycle, may have an obligate hymenopterous parasite, a matter which puzzled Withycombe. The third and final article will deal with the range of habitats species of *Boreus* have entered, the mosses with which *Boreus* species are associated, interpretation of *Boreus* as a winter insect, and a reconsideration of its distribution in relation to drift and glaciation.

Occurrence and Span of Adult Activity

Boreus notoperates has so far been collected at two localities only, both being NW faces of steep canyons, at 1219m altitude (Coldwater Canyon) and at 1645m (Black Canyon), on Mt. San Jacinto, Riverside Co., California. The first is a yellow pine — chaparral ecotone (*Pinus ponderosa* Dougl. — *Adenostoma fasciculatum* Hook. and Arn.) that is Upper Sonoran, or Upper Austral in Merriam's (1898) original sense, the mean temperature for the six hottest weeks (July through mid-August) being ⌣24°C. The second is a mixed woods of yellow pine, incense cedar, white fir and canyon oak (*Pinus ponderosa, Libocedrus decurrens* Torr., *Abies concolor* Gord. & Glend., and *Quercus chrysolepis* Liebm.), fringed and penetrated by chaparral elements; it is Transitional, the corresponding high mean temperature being about 21°C. Over the period 1955 — 71 the mean annual precipitation (close by at the Idyllwild Fire Station, alt. 1645m) was 59.6 cm (23 in.), with 74% falling in the months of November through March during which adult *B. notoperates* have been collected. The adults have so far been found only on mosses growing on boulders and large jointed blocks of diorite, or on snow about them, in both fairly open (chiefly Coldwater Canyon) and shaded (chiefly Black Canyon) situations. Even during the period of winter precipitation the mosses are only periodically dampened and luxuriant, for precipitation is widely scattered, and melts rapidly when snow. The activity of *Boreus* at all its stages coincides with those periods, frequently brief and generally spaced out, when the mosses and their roots are damp. At other times the relative humidity is low, the mosses are dry to the touch, even friable, and their sods

crumbly or powdery. In periods of desiccation *Boreus* are found, if at all, with difficulty, unless a special method is used.

The earliest that adult *Boreus notoperates* have been taken was mid-November, several days following the second snowfall of an inch or more, although it is likely that a snow or a soaking rain in October would bring them forth to judge from laboratory emergences of pupae collected in mid-August. Thereafter adults have been found during the damp periods in all months until mid-March, when they become rare. Air and *surface* temperatures have been mild when adults have been collected, ranging from a low of 6.1°C to 18.3°C, though in the November through March interval below freezing temperatures are not uncommon, mean low temperatures for these months ranging from −4.2°C to 3.2°C, with absolute lows to −12.2°C.

Sex Ratio and Spanandry

The sex ratio among adult *B. notoperates* from field collections, though slightly skewed toward an excess of males early in the season, of females late in the season, does not depart from equality; thus: 131 ♂♂, 150 ♀♀ (of which 32 of each sex were collected as mated pairs); chi-squared gives $0.3 > P > 0.2$. Nor is there a departure from equality among immature stages collected in mid-August and early September. For 47 such larvae and pupae we have:

29 late instar larvae and pharate pupae of which:
19 sexed by dissection of gonads, giving: 12 ♂♂, 7 ♀♀;
10 pupated, giving: 6 ♂♂, 4 ♀♀;
18 pupae when found, of which: 7 ♂♂, 11 ♀♀;

which gives a sex ratio of 25 ♂♂ : 22 ♀♀, for which $0.7 > P > 0.5$.

Now Strübing (1950) has shown from extensive field and laboratory observations that males of *Boreus hyemalis* (L.) do not tend to emerge earlier than females in the autumn. They do, however, tend to die off somewhat earlier than females, and this has been claimed or inferred by others both from field and laboratory observations (*e.g.*, Withycombe 1922, Syms 1934, Cotton 1971; and for *B. westwoodi* Hagen, Brauer 1855; for an undescribed species?, Kolenati 1847)[1]. My own observations on *B. notoperates* are in

[1]Strübing (1950) gives strong reason to believe that Brauer's species is almost certainly *B. westwoodi,* and not *B. hyemalis* as he and others have thought. Furthermore, Pliginsky (1930) states that Kolenati's specimens, from the glacier of Aar (Kazbek, Kaukas), no longer can be found, and are very likely an undescribed species. From Kolenati's comments, they fall among the species with a reduced antennal joint number (~20).

agreement. But it has also been claimed, as early as Hardy's (1848) and MacLachlan's (1868) notes, that the sex ratio of *Boreus* is spanandrous, but only loosely in Marchal's (1911) sense, namely that males regularly make up a minority of the population. Not surprisingly, small collections of *Boreus* may show a predominance of one sex. In general, however, collections of two dozen or more specimens at a locality, but not made at the season's close when females do tend to predominate, give sex ratios which approximate equality, as do those for *B. notoperates.* There are, however, exceptions. But for none of the following records is there a significant departure (namely, $P < 0.05$) from equality of the sexes:

1. *B. brumalis* Fitch	27♂♂	26♀♀	(Hanover, N. H., Cooper, unpubl.)
2. *B. coloradensis* Byers	21	20	(Byers 1955)
3. *B. unicolor* Hine	64	57	(Chapman 1954)
4. *B. hyemalis* (L.)	39	41	(sifting, Druet & Legros, *ex* Lestage 1941)
	33	45	(table 1, to Dec. 20, Strübing 1950)
	103	110	(table 4, *not* text p. 84, Strübing 1950)
	19	11	(Schürmann, *ex* Strübing 1950)
	38	45	(pitfall traps, Cotton 1971)
5. *B. westwoodi* Hagen	60	64	(Martynova 1954)
	24	25	(Martynova 1954)
	12	14	(Martynova 1954)
6. *B. bey-bienkoi* Tarb.	56	49	(Tarbinsky 1960)

As exceptions, with probabilities < 0.02 to < 0.001 as random departures from equality of the sexes, we have:

7. *B. nivoriundus* Fitch	42♂♂	23♀♀	(Hanover, N. H. Cooper, unpubl.)
8. *B. hyemalis* (L.)	398	123	(Steiner 1937)
9. *B. westwoodi* Hagen	97	67	(3 collections, data homogeneous, Fjellberg & Greve 1968)

Judging by records 1–6, and from the proportions among immature stages which have been sexed, the records 7–9, all of which show a significant preponderance of males, may reflect a tendency for

males to wander widely at times in search of females, or true peculiarities of the particular populations, or perhaps of the mode or circumstances of collecting. Strübing's (1950) laboratory rearings of *B. hyemalis* gave 40♂♂, 36♀♀, and Fraser's (1943) account implies that his collection (in September) of pupae of *B. hyemalis* consisted of 29♂♂, 21♀♀ (for which $0.3 > P > 0.2$). My own collection of larvae, pharate pupae, and pupae of *B. nivoriundus* in August, at the same site in Hanover, N. H., at which the adults scored in 7 above were later collected (December to mid-April), gave 30♂♂, 33♀♀. Pupae of *B. brumalis* collected (from October to mid-November) at Princeton, N. J., likewise do not depart from an equality of sexes: 40♂♂, 46♀♀. As Strübing (1950) concluded, the sex ratio in *Boreus* appears to be close to unity for both immature stages and adults, as is the case for *B. notoperates*. The answer to Lestage's (1941) question "is there spanandry in *Boreus?*" must be: "not so far as known, and perhaps not at all," as Lestage suspected. Indeed, the only significant departures so far recorded are in fact *spangynous,* not spanandrous.

Mating

Mated pairs of *B. notoperates* are found chiefly on patches of damp moss, free of snow, from early in November to near the middle of March. Although Fraser (1943) claimed *B. hyemalis* to be crepuscular, there seems to be no special time of day that is favored for mating by *B. notoperates* if the temperature is mild; nor is light a requirement, for *B. notoperates* mates readily in the dark (in an incubator, at 9°C). In but one case (of 33) has a mated pair been found on the snow, and that mated pair had most likely fallen a foot or so out onto the snow from a steep, moss-covered rock-face. Certainly the suggestion that *Boreus* occurs on snow because it is easier to find mates there is implausible; the rule seems to be that mating generally occurs on or in moss, where they congregate when it is available to the insects.

Nine complete matings of *B. notoperates* have been observed, namely from the first attempts of the male to gain a partner to the completion of intromission, as well as a good many partial sequences from all stages in the routine. *B. notoperates* is without a courtship, just as in the three species for which the course of events of mating have been described, namely *B. westwoodi* (Brauer 1855, 1863,

Sauer 1966, perhaps Svensson 1966[2]), *B. hyemalis* (Withycombe 1926, Syms 1934, Steiner 1937), and *B. brumalis* (Cooper 1940, Crampton 1940). From its very onset the affair is between a "coy" female acting as though bent on escape, and an aggressive, though not necessarily persistent, male. An ardent male, when within some millimeters range, springs at the female, ensnaring her with his tong-like wings while seizing whatever he can of her extremities with one or both of his genital claspers (or gonostyles). If he fails to gain a hold, as he occasionally does, the female leaps away and is not directly pursued. Thereafter the male either takes a waiting stance on a sprig of moss, or courses about the moss, in both cases twitching his wings and opening and flexing his gonostyles from time to time.[3] When chance again presents another or the same female, the male attempts once again to gain a firm hold of the female.

When a mating spring has been successful, the male may have seized a female by a posterior femur (5 cases), a mid-tibia (2 cases), a pro-tarsus (1 case), or the antennae (1 case). In some other instances, in which only a part of the mating routine was followed, males had gained holds simultaneously of both a mid- and fore-tarsus, or a fore-tarsus and antenna, or a mid- and hind-tibia, and so on. The initial hold thus seems fortuitous and not limited to a particular appendage or to but one appendage at a time. Depending upon the particular grip of the gonostyles, and the appendage(s) seized, a male may either face opposite to the captured female (7 cases), and may even be chiefly behind her, or face in the same direction as his partner. When a female's femur or tibia has been grasped, a male, without loosening or losing his hold, can generally draw his own body about to a position at right angles to that of the female by forcibly rotating her appendage, but he cannot wholly reverse the direction in which he faced without obtaining an entirely new hold, as he must when initially facing 180° away from his partner.

Once seized, the female's response is immediate and energetic, as though designed to free her from the clinging, intermittently passive, male. She drags the male on his back, his side, or even vertically on his hypopygium, over and through obstacles presented by the moss and debris. Occasionally the male acts to resist, splaying his legs outward as though a drag-anchor, or clutching at the moss, offering

[2]? Also Svensson (1966), whose account must refer to *B. westwoodi,* to *B. hyemalis,* or to both.

[3]Terminology referring to the external male "genitalia" follows Michener (1944).

such resistance to the female as he can. From time to time the female rests, and may even pause to feed at rosettes of young moss leaves. At such times the male becomes enlivened, rights himself, turns the length of his body at right angles to the female's while still holding his original grip with his gonostyles, and swiftly (and repeatedly) arches backward over the female in an endeavor to gain firm grasp of her body with his wings. If he fails and rests, the rebellion of the female returns unabated and continues, as just described, until the male succeeds in subduing her, or she finally rids herself of him.[4]

Should the male succeed in gaining a firm hold with his stiff, spined and hooked wings, he deftly changes grip with his gonostyles so that he now faces in the same direction as the female. Once a position has been attained from which he can rear backward and to the side of the female, and grasp her between her head and mesonotum with his wings, holding her body parallel to his own, he again quickly moves his gonostylar grip forward. Once a sufficiently forward grip with the gonostyles has been gained, the head of the female now being behind the male's forebody, he rears strongly backward a number of times and rakes and manipulates the female's rostrum and antennae with his spined wings as he falls forward again. Should he gain hold of the female's pronotum with his wings, he may move his gonostylar grip from the female's legs to clutch one or both antennae, and then briefly but smartly, drag *her* about by the antennae. Mauling of the antennae is quickly followed by a wholly passive state on the part of the female who thereafter stands as though mesmerized. Surprisingly, on the initial assault in one case, the male seized the female's antennae with his gonostyles; that female thereupon became submissive without a struggle.

When the standing female has become passive, the male (still anterior to the female and gripping an appendage with his gonostyles) again bows backward repeatedly until his groping wings gain a secure hold behind her head, to each side of the pro- or mesonotum, with the female's head pressed sharply and to the side by his flank. The gonostylar grip is then moved as far posteriorly as the male can manage, and the wing grip released. Once the male has the female again firmly gripped with his wings, and the gonostyles reach sufficiently far backwards, he tries to seize the ovipositor with his gonostyles; ordinarily several attempts are required, and after each failure

[4]Maréchal (1939) misremembers Lestage's (1920) account when he states "c'est la ♀ qui saute sur le ♂, celui-ci cherchant à fuir et a s'en débarasser!", and goes on to tell still more of female sexual aggressiveness.

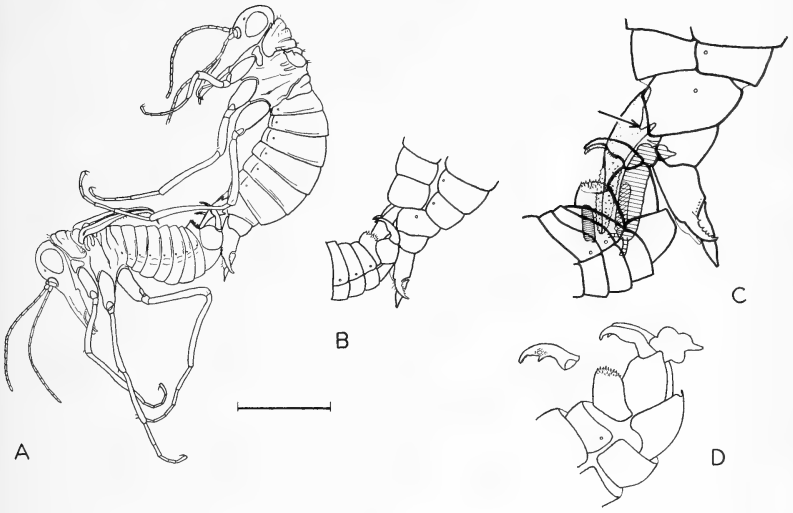

Fig. 1. Mating of *Boreus notoperates*. A, mated pair preserved in female perpendicular position; the medial tooth of the gonostylus has disengaged (at death) from the lateral basal notch of the gonapophysis. B, full union of male and female; medial tooth of gonostylus seated into the lateral basal notch of the gonapophysis; C, semi diagrammatic representation of mated specimens cleared in clove oil; as in A, the gonapophysis is partially withdrawn from the endandrium, and the lateral basal notch of the gonapophysis (at arrow) is clearly visible; dorsal proctigeral plate (closely, transversely lined) lies within epandrial notch; gonapophyses stippled; aedeagus (widely, transversely lined) partially inserted in common oviduct — note flap at anterior margin of female gonopore and paired ejaculatory ducts entering base of aedeagus; the sclerotized lamina that forms floor of endandrium is cross-hatched (see text). D, male terminalia with everted aedeagus, apical nipple of which bears the gonopore; upper left — inner face of right gonostyle to show median tooth and stylocavernula. All from camera lucida sketches; scale: for A and B equals 1 mm, for C and D equals 0.5 mm.

the gonostyles are returned to a grip on the posterior legs, near the coxae, and the male rests. When at last the ovipositor has been grasped, the gonapophyses are pried down and slightly apart, the female holding them, as though plastic, in whatever position they were released by the gonostyles. The gonapophysis of each side is then engaged between the inner tooth and the tip of the corresponding gonostyle which, on adduction, directs and thrusts the tip of the gonapophysis into a pocket ventral to the epandrium (see below). Ratchet-like, the two gonapophyses together are worked down and in by the gonostyles. Finally each gonostyle becomes securely seated on the corresponding gonapophysis, for its inner tooth (figs. 1D; 2A, B)[5] engages the lateral notch of the gonapophysis near its base (fig. 1B, compare with 1A and C, arrow).

The female is then released from the clasp of the male's wings. Thereupon she rocks backward 90° or more, with rostrum and antennae folded between the forelegs, femora drawn up to the sides, tibiae adducted, tarsi drooping — the "death-feigning" posture that concludes the leap of a startled *Boreus*. Surprisingly, the female thereafter remains vertically in that posture, though her legs relax, and the male folds his wings to their usual rest position over the back, fig. 1A). In side view it can be seen that the tip of the aedeagus has been fully inserted into the common oviduct (fig. 1C). Despite the unbalanced appearance of a male and female united thus at a right angle, without any noticeable difficulty the male may run, climb, feed, and hop, landing without loss of balance. If startled, the male may leap several centimeters or more, landing in (or assuming) the death-feigning posture, motionless and resting on his flank; the female too death-feigns as before; after a few moments, the male returns to his feet.

In all, ten cases have been timed from the first assault of the male to intromission; these took from 6 minutes to 18, with a mean of 13 minutes (all at 17°–20°C). The total duration of intromission has not been timed, but I have observed cases in which it was less than an hour, others of more than several hours. Both sexes mate repeatedly, with the same or different partners.

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[5]Esben-Petersen (1921) was unable to see this median tooth in specimens before him of *B. brumalis* and *B. nivoriundus;* Lestage (1940) took the supposed absence of a median gonostylar tooth as presenting a cardinal character for *Euboreus,* a genus he erected for all American species. For discussion of *Euboreus,* see Cooper (1972).

Discussion of Mating

The events just described are different in a number of significant features from those in the matings of *B. hyemalis, B. westwoodi* and *B. brumalis,* which are alike. Once a female of those species has been seized by a male, it ordinarily becomes passive (but *not* always, see Syms 1934, Aubrook 1939, Sauer 1966, Crampton 1940). The rested male then grips the female across the midbody with his wings (as does *B. notoperates*), and with them and his gonostyles works her body over his dorsum so that it is axially symmetrical and parallel to his own. The gonapophyses are then pried down and inserted into the subepandrial pocket, the wing-hold is released and the female rocks back until perpendicular to the male. Intromission very likely occurs at this point, as it does in *B. notoperates.* The relative station of the two sexes just prior to intromission, or the "pose" (Lamb 1922), in all four species is truly a *"female vertical pose"* with (presumably) an inverse correlation of the genital conduits of the two sexes.[6]

Now Lamb (1922) used "vertical" as a contrasting term to "linear" (or tail to tail) to denote arrangements of partners in which one partner is above the other. In the overwhelming majority of such cases, the body of the upper insect lies more or less parallel to that of its partner. Consequently I shall call the *pose* common to the four *Boreus* a "female perpendicular pose" to distinguish it. The final copulatory attitude of *B. notoperates* does not depart from the pose; accordingly it is a "female perpendicular position" (fig. 1A). In contrast, *B. hyemalis, B. westwoodi, B. brumalis, B. californicus* (= var. *fuscus* Carpenter?) (Cockle 1908, 1914), *B. nivoriundus* Fitch (Carpenter 1936; Cooper, unpubl.), *B. unicolor* Hine (Byers 1954) and *B. vlasovi* Martynova (Vlasov 1950), namely in *all* other species for which the copulatory position has been recorded, the final attitude differs from the pose, being a female vertical position.[7]

[6]On intromission, the apparent dorsal wall of the aedeagus of *Boreus* lies in contact with the ventral wall of the common oviduct, hence in "inverse correlation", which is unusual (fig. 1C). In most insects correlation is "direct", or symmetrical, for contact is dorsal-dorsal and ventral-ventral; in many insects having a vertical position, direct correlation is brought about by rotation of the male genital tract (see Lamb 1922).

[7]For original drawings, or photographs (reference in boldface), of copulating pairs in their final female vertical position, see: for *B. hyemalis,* fig. **3**, pl. 8, Withycombe (1922), fig. 1, Steiner (1937), fig. **7**, Strübing (1958); for *B. westwoodi,* fig. 5, pl. 3, Brauer (1855), fig. **2**, Sauer (1966); for *B. brumalis,* fig. 9, Cooper (1940), fig. 1, Crampton (1940).

On the basis of its morphology, *B. notoperates* (along with the similar *B. brevicaudus* Byers) has been adjudged the least primitive of all known species of *Boreus* (Cooper 1972). Interestingly, its mating stands apart from that described for the other three studied species: at its onset (the enduring resistance by the female), at its midpoint (submission by the female only after antennal "abuse"), and at its very end (a female perpendicular position derived without change from a similar pose). In that last attribute, it differs from all seven other species of *Boreus* for which the position has been recorded and, notably, that position is alike in all seven. The long period of female coyness and the need for manipulation of the female's antennae go hand in hand, but I cannot decide whether these are primitive aspects or not. But the female perpendicular position is almost certainly a specialization, the marked change from pose to position that occurs in other species of *Boreus* most likely being primitive. I suspect that the presumed loss of change is related to the unusually shortened ovipositor of *B. notoperates* and the relative depth to which the gonapophyses are inserted into the male; if that is so, *B. brevicaudus* may be expected to have a female perpendicular position, and possibly also the remote *B. chadzhi-gireji* Plikinsky as well.

Because most *Boreus* follow closely similar mating patterns, as do *B. brumalis* and *B. nivoriundus,* with poses and final positions that are alike, the question quite naturally arises as to whether cross-matings occur or are even attempted. My own trials on this score were with smallish *B. nivoriundus* males and *B. brumalis* females, two species quite frequently found within common areas in New Hampshire. They showed no mutual interest whatsoever. This was not to be attributed to lack of potential competence or sexual aggressiveness on the part of the males for, when female *B. nivoriundus* were added, the males soon paired, or attempted to do so, with the females of their own species. Perhaps the scent or secretion claimed for female *Boreus* (Hardy 1848, Withycomb 1922, Maréchal 1939) has a role as a species specific mating pheromone.

The Anatomical Correlations in Mating

The female vertical position is widespread among insects, yet not common. It has been recorded for Orthoptera (where it, or its equivalent, the "false male vertical position" of Richards, is the usual mode), Plecoptera, Mallophaga, Anoplura, Mecoptera, Siphonaptera,

Diptera (as *Empis*), and Coleoptera (*Lomechusa*) (Meisenheimer 1921, Richards 1927), as well as for aradids (Heteroptera) (Usinger and Matsuda 1959). For the majority there is little information on the correlation involved, but it is probably generally inverse, with the anus of the female unobstructed, as in *Boreus*. The similarities cease here, however, for so far as I am aware the species of *Boreus* are unique in their adaptation to, and practice of, a reciprocal intromission — namely a concurrent passage of the female's gonapophyses into a specialized genital pocket within the male, and of the aedeagus into the common oviduct (fig. 1C). This curious arrangement was first commented upon by Cockle (1908, 1914), and later by Steiner (1937) and Cooper (1940), but it has not properly been described.

Projecting cephalad from the medio-dorsal aspect of the gonocoxites of the male, there are two sclerotized laterally flattened straps, the dorsal apophyses of the gonocoxite, that expand medially and unite to form a thin, broad, pigmented roofing plate that lies below the anus (figs. 2A, B; fig. 4, Cooper 1972). The more dorsal anus is itself enclosed by sclerotized dorsal and ventral proctigeral plates (segments X + XI?) (fig. 2A; fig. 3, Cooper 1972).[8] Ventral to the gonocoxital roofing plate, or dorsal portion of the gonobase, there is a broad, sclerotized band overlying the dorsum of the aedeagus (figs. 1C, 2A, B; also fig. 4 Cooper 1972). A wide, enclosed, shallow but elongated pocket is thus formed between the dorsal gonobase, the muscles of the gonocoxites, and the sclerotized band over the aedeagus. In the unmated male at rest, this pocket (which I call the *endandrium*) curves downward under the epandrium (fig. 2B).

Just prior to insertion of the aedeagus, the gonapophyses (sternites-VIII, or "ventral valves of the ovipositor") are thrust by the male into the endandrium. The main fields of caudally-directed spines on the bosses to each side of the epandrial notch (fig. 2A) catch on the outwardly directed denticles of the blades of the gonapophyses, preventing slippage outwards as the gonapophyses are initially forced, ratchet-like, more and more deeply into the endandrium. Once fully inserted within the endandrium, the gonapophyses are locked in place there by the gonostyles of the male. Not only is the blade of each gonapophysis grasped tightly between the apex and inner tooth of a gonostyle, but that inner tooth of each gonostyle is in turn engaged by being seated into the lateral basal notch of its corresponding gonapophysis (fig. 1B *cf.* A, C, arrow). That union so forcibly locks the

[8]The proctigeral plates (= segment-XI) in the female of *Boreus notoperates* are similar to those of *B. brevicaudus,* described by Byers (1961).

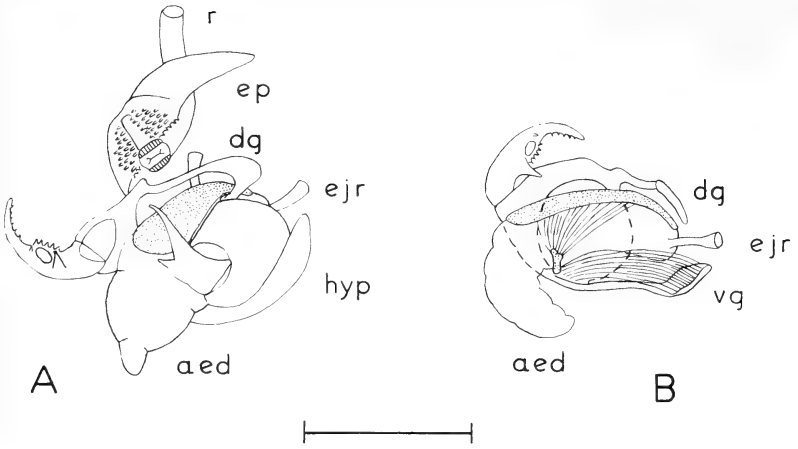

Fig. 2. Genital anatomy of male *Boreus notoperates*. A, terminalia viewed obliquely from the right side. The epandrium (ep), or tergite-IX, has been separated from its articulations on the right, and reflected about 60° to the left. The anus, enclosed by proctigeral plates (cross-lined) lies immediately below the epandrial notch, the spined epandrial bosses to each side. Gonostyles abducted on right, displaying in profile the short, sharp medial tooth which engages the lateral basal notch of the gonapophysis. The dorsal gonobase (dg) extends anteriorly from the gonocoxites, flaring out as the roof of the anterior end of the endandrium. Median plaque (stippled) immediately over the aedeagus forms the floor of the endandrium; aed — partially everted aedeagus, ejr — right ejaculatory duct, hyp — hypandrium, r — rectum.

B, partially exserted aedeagus (aed), right lateral view. Epandrium, proctiger, right gonocoxite and hypandrium have been removed. Above, dg, the left dorsal half of the gonobase; below, vg, the left ventral half of the gonobase. Sclerotized plaque (stippled) overlying the aedeagus joined by a fan of muscles to U-shaped sclerite (stippled) partially encircling the aedeagus ventrally. The genital chamber is the space enclosed between the dorsal and ventral gonobases, the endandrium lies between the dorsal gonobase and the sclerotized plaque, and the aedeagal chamber lies between the sclerotized plaque and the ventral retractor muscle attached to the ventral gonobase; ejr — right ejaculatory duct. Both figures from camera lucida drawings; scale equals 0.5 mm.

mated pair together that, unless the male's grip is loosened, the female cannot free herself. In all but *B. notoperates,* the female is then rocked forward into the final female vertical position. Although the spines of the epandrial bosses may once again act against denticles of the gonapophyses' blades, preventing slippage, and the male's wings give an added grip, the change in position seems a supererogation so far as security of the male's mating grip is concerned.

The aedeagus, at rest, lies within a chamber that may be distinguished from the endandrium. The roof of the aedeagal chamber is the band-like sclerotization over the aedeagus which forms the floor of the endandrium; the side walls are in part defined by the internal faces and musculature of the gonocoxites, and the floor of the chamber by the cephalad-directed apodemal band from the antero-medial, ventral angle of each gonocoxite that joins its homolog as a broadening, very thin strap, the ventral gonobase (fig. 2B) which, in some specimens, encloses a minute medial sclerotized plaque. The space enclosed between the dorsal and ventral gonobases, then, forms the genital chamber proper, and the endandrium and aedeagal chambers are thus dorsal and ventral subdivisions of it.

The aedeagus itself is a heavily muscled tube containing the unpaired ejaculatory duct. At rest it is hook-shaped, with its hooked tip wholly withdrawn into the aedeagal chamber, resting upon the ventral adductor muscle (fig. 2B). The paired ejaculatory ducts separately enter the caudal end of the aedeagus (figs. 1C, 2A, B), uniting within it. Above the aedeagus is the sclerotized band that serves as floor to the endandrium. Below, near the point at which the aedeagus bends back on itself in its distal third, there is a slender, sclerotized hoop which partially encircles the aedeagus on the ventral side, from which a fan of muscles extends dorsally and caudally to insert on the dorsal sclerotized band. In *B. borealis* Banks,[9] and *B. coloradensis* Byers, there is both a dorsal *and* ventral sclerotized longitudinal band between which the aedeagus lies.

The contraction of the muscles running from the ventral hoop to the floor of the endandrium both enables the aedeagus to be held and packed in retraction within the genital chamber and, when the aedeagus is everted, to reduce the space of the aedeagal chamber and thus force the aedeagus caudally outward. No doubt, to judge from the anatomical relations of the endandrium, the initial downward

[9]The Whitney's field-notes suggest that Banks, when describing *B. borealis,* had but two of a total of four specimens that were captured; see records 129 and 157, pp. 136-137, in McAtee (1923).

thrust and pressure of the gonapophyses in the endandrium are additional (perhaps necessary) factors in the eversion and erection of the aedeagus. Contraction of the annular musculature of the aedeagus itself additionally extends the organ and causes the tip to inflate into a bulb, bilobed dorsally, which abruptly terminates in a conical, or nipple-shaped tip upon which the ejaculatory duct opens (fig. 1D). The fully extended aedeagus runs between, and is guided by, the smooth inner faces of the gonapophyses and the ventral surface of the ovipositor to enter the common oviduct, from the anterior ventral margin of the orifice of which extends a chitinous guiding flap that, at other times, closes the aperture (fig. 1C). Once entered into the oviduct, the apical bulb of the aedeagus is inflated within the vestibule of the common oviduct which opens at the junction of segments IX and X. In that position the ventral bulge of the bulb evidently blocks off the common duct of the tubular accessory glands of the oviduct, and the conical tip of the aedeagus enters the short spermathecal duct, within which there is a minute sclerotization (fig. 9, Cooper 1972). Insemination therefore takes place directly into the duct of the spermatheca.

The account just given will very likely be found to agree in its main features with the complex "reciprocal intromission" of other *Boreus,* even though Martynova's (1954) figures 1–6 hint that the endandrium may differ in depth and conformation among different species. However it is at variance with Steiner's (1937) description (or inference?) for *B. hyemalis* in which the tips of the gonapophyses are said by him to be received directly and separately into the pockets of the epandrium. That is not the case in still other mated *Boreus* (*B. brumalis, B. nivoriundus*) that I have studied, and in which endandrial insertion occurs. Nor is it likely that the condition observed by Byers (1954) in a preserved, mated pair of *Boreus unicolor* Hine is a normal state of affairs; namely that the tips of the gonapophyses are bent across one another, and are held thus by the gonostyles of the male at right angles across his epandrium. Nor does *B. notoperates* conform to Potter's (1938b) description for *B. hyemalis* of a coiled or folded ductus ejaculatorius (see her fig. 30) which, at rest, is thrown into three flexures within the genital chamber, and which is *evaginated* during coition. As Steiner said, the intromittant organ is strongly muscular, and as I have shown it is in effect erected without evagination comparable, say, to that of a true internal sac. The element which Potter figures in front of the first distal flexure, appearing continuous in her figure with the "ejacula-

tory duct," is very likely the large retractor muscle in my figure 2B which occupies that position in *B. notoperates*. Brief comment on the aedeagus of *Boreus* will be found in Fitch (1847), Kolenati (1847), Cockle (1908, 1914), and Byers (1954), as well as in Withycombe (1926) and Crampton (1918, 1920, 1923, 1931) who have figured it in an everted state. To judge from these figures and my own, species of *Boreus* may differ in the apical morphology of the aedeagus.

Cytology

Boreus notoperates has a diploid number of 20 in the female and 19 in the XO male. At spermatogenesis, the autosomes are conjoined by chiasmata (nearly always but one per bivalent) that are interstitial or proterminal at diakinesis, but for the most part terminalized by metaphase-I. There is only a moderate premetaphase stretch.

The acrokinetic X is the largest chromosome of the set (from 7–9 μ long), being respectively two to five times the lengths of the largest and smallest autosomes. The X possesses a nucleolus organizer proximally in the long arm. Spermatogenesis is orthodox, the X segregating precociously and reductionally at anaphase-I. At anaphase-II, as at anaphase in both spermato-and oogonial mitoses, the separating chromatids of X stretch and span the entire length of the elongating spindle before their distal tips disjoin.

The chromosome number of *B. notoperates* is the lowest so far known for *Boreus* (*B. brumalis*, n♂ = 11 + X_1X_2,Y; *B. hyemalis*, n♂ ∽ 14 + X,O; *B. nivoriundus* n♂ = 15 + X,O; Cooper 1951 and unpubl.); except possibly for a cytological form of *Nannochorista dipteroides* Till. (n = 9 ?, Bush 1967), it is indeed the lowest number so far claimed for Mecoptera. A second strain of *N. dipteroides* (n = *ca* 14), *Chorista australis* Klug. (n♂ = 14 + X,O) (both in Bush 1967), and three species of *Bittacus* (n♂ = 13 + X,O; n♂ = 14 + X,O; n♂ = 15 + X,O) (Matthey 1950; Atchley and Jackson 1970), all lie within the range of *Boreus*. My preparations of a single male of *Merope tuber* Newm. display chiefly very drawn-out early diakinetic chromosomes, and are sufficient only to establish that it is XO, chiasmate, and has a haploid number that is less than n♂ = 12 + X,O — possibly n♂ = 10 + X,O. Though, at this time no more definite statement can be made for our most primitive mecopteran, it is nevertheless clear evidence that the chromosome number of *Merope* is not a relatively high one. On the other

hand, the seven species of *Panorpa* so far reported upon by Naville and de Beaumont (1934), Kichijo (1943), Ullerich (1961), and Atchley and Jackson (1970) stand apart, having the highest chromosome numbers known for Mecoptera; they are: n♂ = 20 + X,O, n♂ = 21 + X,O, and n♂ = 22 + X,O (4 species, plus one with n♀ = 23).

The cytology of *Panorpa* is thus characterized by two evolutionary differences from most other Mecoptera now known: absence of chiasmata at meiosis in the male, as Ullerich (1961) first demonstrated, and unusually high diploid numbers. Whether or not male Nannochoristids and Choristids have chiasmata is not known, although Bush's (1967) account indicates that male *Nannochorista dipteroides,* like Panorpids, may have a meiosis without chiasmata.

Despite the strongly derived nature of the external morphology of Boreids, and especially of *Boreus notoperates,* therefore, their chromosome numbers and possession of chiasmata at meiosis in the male appear conservative. Congruent also with a primitive state is their possession of panoistic ovarioles, as is known also for *B. brumalis* (Cooper 1940) and *B. nivoriundus* (unpubl.). It is likely that this is the case also for *B. hyemalis;* Steiner (1937) could find no nurse cells in its ovaries, but was undecided as to whether the ovarioles are panoistic or meroistic.

Oviposition

As commented above, both male and female *Boreus* mate repeatedly and with varied partners. In *B. notoperates* the spermatheca of the female has some 24 sperm receptacles (fig. 9, Cooper 1972), all of which come to be filled with spermatozoa. The natural promiscuity may be seen as tending to reduce close inbreeding within the small, scattered populations. In the laboratory, females lay within two weeks following their first mating, and perhaps within a few days as is the case for *B. hyemalis* (Strübing 1950, 1958).

The large majority of the eggs at laying (which measure from 0.5 to 0.6+ × 0.3+mm, length by width)[10] by *B. notoperates* are placed singly, vertically, and ordinarily at such a depth that the apex of the egg lies from 0.1 to 0.3 mm below the surface of the sod of the moss, amid its rhizoids. Sixteen females, over a period of ten days at 21°C, laid 186 eggs that I was able to locate — assuredly a

[10]The egg widths in Cooper (1972), p. 275, should of course be 0.31 mm and 0.30 mm respectively.

minimal number — giving an average of 1.16 eggs per day per female. The span of life of a female in such cultures was no more than four weeks. Were such a rate of laying maintained, a laboratory-held female would be expected to lay about 32 eggs. At death, these females possess mature eggs in their ovaries, and so their potential fecundity is higher than just estimated. These experiences are in line with those of Withycombe (1922) and Strübing (1950, 1958) for *B. hyemalis,* although their estimates that the average female lays a maximum of ten or so eggs in a lifetime I suspect to be much too low, considering the hazards of egg development, larval life, and the full two-year life cycle that must be met. Females of *B. brumalis* and *B. nivoriundus* which I have dissected at the close of their seasons in late February and March, still have a few mature eggs in their oviducts, as Strübing (1950) found for *B. hyemalis,* but in some there is widespread involution of follicles within the ovarioles, the epithelium of the egg chambers incomplete, with many nuclei lying within large protoplasmic masses that simulate nurse cells.

I have not witnessed oviposition, but Brauer (1855, see fig. 5, plate III), Aubrook (1939) and Maréchal (1939) have described females, nearly perpendicular, with ovipositors buried in the soil. Only Svensson (1966), however, has witnessed actual oviposition (perhaps in *B. westwoodi,* as in Brauer's case), and described the passage of the egg along the incomplete tube formed by the gonapophyses and tergite-X. When the egg reaches the tip, the cerci are flexed ventrally, forcing the egg out onto the ventral surface of the gonapophyses. The egg is thereupon set down upon a moss stem, the whole process taking 3 to 4 minutes. It is to be noted that the female he observed laid 4 eggs within a period of two hours, lending some credence to the belief that females of *Boreus* may actually lay at least again as many eggs as Strübing estimates for the total production of a female *B. hyemalis.* Indeed Strübing (1950) records one clump of seven eggs, presumably laid by a single female. Certainly it is reasonable to assume that laboratory conditions are not ideal for oviposition, and that such estimates do represent minima.

Hatching

Hatching occurred in laboratory samples of eggs of *B. hyemalis* within 8 to 10 days, at 8.8°C, with about 50% mortality in Withycombe's (1922) series; in contrast, Strübing's (1950) samples took from 3 weeks at approximately 20°C to as long as one and a half

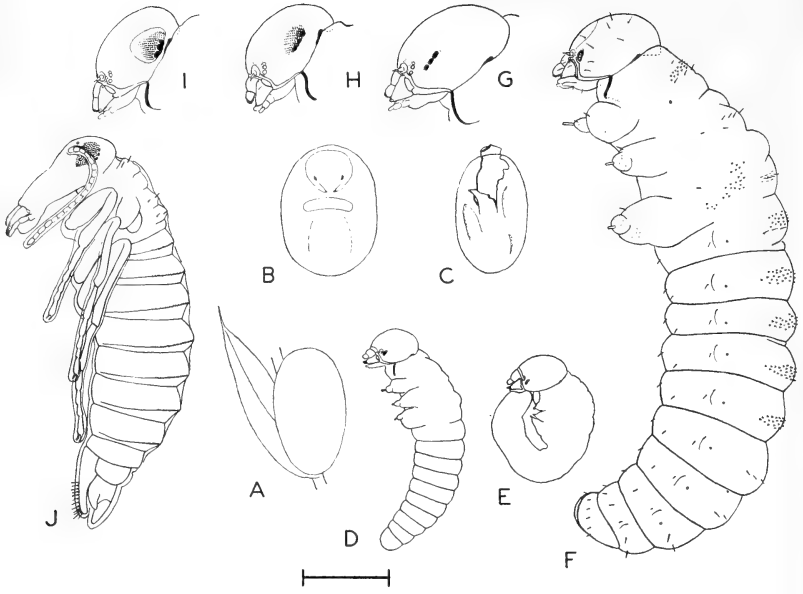

Fig. 3. Immature stages of *Boreus notoperates*. A, freshly laid egg. B, egg just before hatching — note larval head, transverse band, margins of reflexed end of abdomen. C, rent chorion following hatching. D, first instar larva. E, first instar larva dissected from egg at stage comparable to B. F, last instar larva — especially note conformation of pigment underlying stemmata (KOH preparation). G to I, pharate pupal heads — note change in both position and conformation of eye pigment, and its relation to the development of the imaginal eye. J, pharate adult female — note connections between imaginal fixed setae of gonapophyses and corresponding setae of pupal exuvium. Scale = 0.5 mm, applies to figs. F through I; scale = 1 mm for J; for dimensions of eggs and first instar larvae, see text.

months at 7°C, and 44 of 46 eggs of her series hatched. In the case of *B. notoperates,* two of four eggs kept at 20°C hatched in a period of 24 days; the other two were at the stage of hatching at that time, but the larvae died without perforating the chorions.

The four freshly laid eggs of *B. notoperates* which I followed swelled, in the first 15 days, from 0.5 × 0.3 mm to 0.66 × 0.46 mm — 0.68 × 0.50 mm, at which time the larval head, pigmented eyes, jaws (mostly held open, but moving from time to time), and reflexed abdomen could be seen, as well as a grayish, transverse band that had appeared on or near the chorion below the larval head (figs. 3B, E).

By the next day (day 16) the larvae moved occasionally within the chorions. By day 18 the larval gut appeared swollen and gray. Over the next five days the larvae became very active, even reversing their positions within the eggs; at times the chorion of an egg would collapse inwards, only to reinflate once again. On the 24th day two of the larvae hatched by means of great rents torn through the chorion (fig. 3C). I did not observe the emergence, or how the chorion was torn open. As there is no egg burster such as Gassner (1963) has described for the first instar larva of *Panorpa nuptialis* Gerst., it is possible that infolding of the chorion, as earlier observed, enables the larva to seize and rip the chorion with its jaws, or that the gray band on the chorion is associated with a local weakness. Strübing (1950) has described the swelling of the developing egg (which also occurs in other Mecoptera, see Currie 1932, Setty 1940, Byers 1963), and the hatching of *B. hyemalis* which takes but 10–12 minutes; the events prior to hatching are similar to those of *B. notoperates*.[11]

The newly hatched larva of *B. notoperates* (fig. 3D) is dead white, except for the pale amber head capsule, darker jaws, and pig-

[11]Some 127 developing eggs of *B. notoperates* were at hand when this passage was written (Feb. 1974). Subsequently they were divided into two lots of which one (of 88 eggs) was followed daily to hatching. All had been kept at 9°C, and were at a mean age of approximately 30 days when removed to 20°C for observation. They had all undergone swelling, but no other sign of development was discernible. The smallest egg was 0.58 × 0.44 mm, the largest 0.78 × 0.52 mm, and the most distended in girth was 0.64 × 0.56 mm. In what follows, day 0 is the day of removal (Jan. 14, 1974) to 20°C.

At day +15 eyes were visible in nearly all eggs; at +21 heads pale testaceous, eyes black, mandibles very dark and active; most eggs alike in stage — despite this, hatching spread out over a period of 36 days.

Hatch was 93% (82 of 88 eggs; 2 did not mature, 3 failed to hatch but had had active larvae, 1 killed by mold). First egg to hatch was at +25 days, half of the eggs had hatched at +31, three-quarters at +33, 90% by +38, and the last on +61.

Unlike the mandible of the last larval instar, that of the unhatched larva has a sharp, falcate, apical tooth, a moderately long, sharp, subapical tooth, and two successively smaller, sharp denticles. When hatching commences, the turgid chorion is abraded, then penetrated, by the mandibles, whereupon it collapses somewhat and folds inward to a varying degree, owing to loss of fluid from the egg. Within an hour, or as long thereafter as several days, the larva emerges. It does so by cutting through the fold, and elsewhere, to produce a broad apical flap, or even a free cap to the egg. By peristaltic movements, especially of the thorax, the larva forces the flap and emerges through the gaping hole in the chorion in a matter of ten to twenty minutes.

mented eyes. It has a head width of 0.28 mm, widest girth across the thorax of 0.3 mm, and a body length of 0.9 mm. It is not provided with abdominal prolegs, as described by Brauer (1855, fig. 7, pl. III; 1863, fig. 2, pl. XIV) for *B. westwoodi,* but the terminal abdominal segment does serve, and very effectively so, as a holdfast as he believed.

The two hatched larvae were placed on a small mat of damp moss into the sod of which they speedily disappeared. Seventeen days later the larvae were torpid, stretched out and turgid, and remained so for the next four days. At that point the head capsule was 0.3 mm wide, the metanotal girth 0.38 mm (the broadest portion of the thorax), and the total body length 1.04 mm in one, 1.42 mm in the other. If, at this point, they were ready for the first larval moult, then the first instar is completed within 16 to 17 days at 20°C. Unfortunately observations had to be discontinued, and the larvae were preserved.

Strübing (1950, 1958) has shown that the rate of development in *B. hyemalis* is strongly affected by temperature and, unlike the adult, eggs and larvae develop only very slowly, if at all, at the low temperatures of winter. Indeed the egg remains dormant through the winter months, normally hatching in the period from the end of March to mid-April. Hatching is almost certainly earlier in the case of *B. notoperates* for, by the close of January and February, air temperatures above 20°C and warm sunshine are not uncommon in its habitat on Mt. San Jacinto.

Larva

During the last two weeks of August and in September, larvae, pharate pupae (Hinton 1971, 1973), and pupae of *B. notoperates* are found in the sod of host mosses, amid the rhizoids. The apparent larvae are of two size classes: (1) with a mean head length from the tip of the labrum to the occiput of 0.49 mm, range 0.47–0.52 mm, and a coefficient of variation (V) of 5.7 (6 specimens), and (2) with a mean head length of 0.68 mm, range 0.59–0.87 mm, and a surprisingly large V of 9.7 (23 specimens). Though smaller larvae of the second class proved to be males, and the larger females, the size distribution is not bimodal. No doubt their high coefficient of variation is in part a consequence of two factors: a sexual difference in size at the last instar, and the consequences of the larval-pupal apolysis that closes the larval stage and which I did not detect until later. They proved a heterogeneous lot of last instar larvae and pharate pupae.

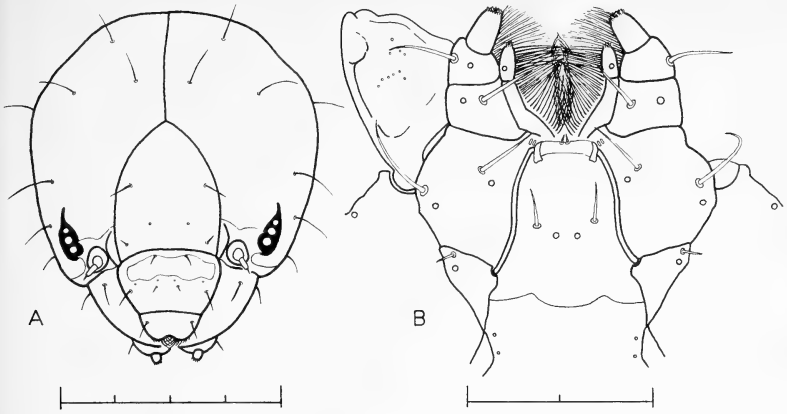

Fig. 4. Head of last instar *Boreus notoperates.* A, frontal view. B, mouthparts in ventral aspect. For details see text. Full scale = 0.4 mm for A, = 0.2 mm for B.

The number of larval ecdyses is not known for any species of *Boreus,* but it is very likely four as in other species of Mecoptera (Currie 1932, Setty 1940, Byers 1963). The ratio of the mean head length of the larger larvae and pharate pupae to that of the smaller larva is 1.38. This gives estimated head lengths for the two immediately preceding larval stages as 0.36 mm and 0.26 mm respectively. As the head length of the first instar larva is known to be 0.32 mm, the series ends there and the number of instars is thus very likely four. The probable Dyar constant of 1.29 (which is low compared with Byer's figure of 1.46 for *Panorpa nuptialis*) gives a calculated head length of 0.41 mm for instar-2, of 0.49 mm for instar-3, and of 0.68 mm for instar-4. Strübing (1950) left the matter of the number of larval instars of *B. hyemalis* open. Withycombe (1922), also unable to find larval exuvia, judged from head capsule growth that there are at least four instars. Though Strübing's measurements of larval head capsules are in fact heterogeneous, they are reasonably well satisfied by a Dyar constant of 1.34 and four instars.

The full grown larva of *B. notoperates* is remarkably similar to the first instar larva (compare figs. 3D and F). The head is pale amber in color, the body white to pale yellow, and in life it ranges from 2.6–3.7 mm in length. In shape it is "scarabaeiform," to use Peterson's (1951) characterization of the larva of *B. brumalis.* As

illustrated (fig. 3F), the larva of *B. notoperates* has localized patches of denticles on the dorsum of the pronotum, a transverse row of setae on the mesonotum, two rows of setulae enclosing a row of setae on the metanotum, an oblique scattering of denticles on the flanks of the metanotum, and patches of denticles on each of the indistinctly 3-segmented legs. Abdominal tergite-1 has a dorsal transverse patch of denticles behind which stands a row of setae. Abdominal tergites-2 through 5 have dorsal, transverse patches of denticles, and each segment thereafter possesses only a transverse row of setae, except for segment-10 which is encircled by a row of setae. Though not appearing unusually modified, the apical abdominal segment serves, as in the first instar larva, as an adhesive holdfast. Denticles and setae alike are pale testaceous. As usual for Mecoptera, there are 9 spiracles: one on the flank of the pronotum, and one on each of abdominal segments-1 to 8.

The larval head (fig. 4A) is convex and more or less ovoidal in face view. At the bases of the mandibles, lower halves of the antennal sockets, on the transverse sclerotized plaque on the proximal portion of the clypeus, the head is bright castaneous, as are the mandibles (except for their piceous tips and the cervical sclerites), all contrasting markedly from the pale ground color. The eyes possess three stemmata, the lower two of which have very convex lenses while the uppermost is smaller, flat and somewhat atrophied. Underlying and surrounding the stemmata is a distally attentuated patch of black pigment. The antennae have two obvious segments, and terminate in a bristle-like prolongation that may or may not be a true segment. Coronal, frontal and epistomal sutures are well marked and complete. The clypeus is roughly trapezoidal, the labrum apically emarginate; together they conceal the biting edges and tips of the closed mandibles.

Almost all of the setae described and designated by Boese (1973) for the larval head of *Panorpa* species are to be found, similarly situated, in *B. notoperates.* The differences between *B. notoperates* and *Panorpa* species lie in the absence in *Boreus* of a pair of setae (SO) immediately dorsal to the eye, the presence of but a single pair (instead of 2 pair) of setae (SI) on the labrum which, in addition, are not marginal as in *Panorpa,* the presence of but a single pair of setae on the mandibles (instead of 3), and the possession of an *extra* pair of setae, lacking in *Panorpa,* on the proximal edge of the medial third of the sclerotized clypeal band, just below the epistomal suture. In view of the notable differences between *Boreus* and *Panorpa* in

other aspects of larval and adult anatomy, the complex setation of the larval head appears to have been remarkably stable.

The mandibles of *B. notoperates* (fig. 4B) are massive, triangular, strongly sclerotized, and thrown apically into three, poorly demarcated, blunt teeth. Maxillae and labium are membranous. The maxillary cardo is triangular, the stipes large and trapezoidal, the palpifer (which seems a basal palpal joint) cylindrical and surmounted by the subequally 2-jointed maxillary palps, the terminal joint of which is cylindrical and densely papillate apically. A brush of closely set long hairs is directed medially from each maxillary lobe. The 2-jointed labial palps are slender and very elongate. Like the maxillary palps, they are testaceous, and bear a cluster of small pegs at their tips. The prementum, which is strap-like and sclerotized, bears two stout, convergent setae medially at its anterior margin. The submentum is large, trapezoidal, and broader posteriorly.

The numbers and arrangements of setae on the submentum, prementum, basal joint of the maxillary palpi, and possibly of the cardo, are similar to those figured by Potter (1938a) for *B. hyemalis*. *B. notoperates,* however, appears to have one less seta on both the palpifer and stipes, and the conformation of palps, maxillary brushes, prementum, and mandibular teeth differ strikingly from that species. It also differs from *B. hyemalis* in shape of head, the presence of a complete frontal suture, a distinct epistomal suture, a sclerotized clypeal band, emarginate labrum, and details of setal pattern. Brauer's (1855, 1863) descriptions and figures of *B. westwoodi* do not permit a comparison with *B. notoperates,* but I agree with Potter (1938a) that there is no spinneret on the labium as Brauer considered possible and as Withycombe (1922) claimed. If Brauer is correct that the labial palps of *B. westwoodi* are 3-jointed, that is a very striking difference from *B. hyemalis* and *B. notoperates*. Peterson's (1951) brief description and figures are sufficient to show that the larva of *B. brumalis* has notable differences from both *B. hyemalis* and *B. notoperates* in head shape, labrum, sutures (only an epistomal suture is figured), and setal distribution and lengths on both head and body.

It is important to emphasize that presence of a distinct epistomal suture in the larvae of *B. notoperates, B. brumalis,* and *B. westwoodi,* because its supposed absence in *Boreus* is one of the characteristics emphasized by Hinton (1958) as a feature of Crampton's (1930) suborder Neomecoptera, only diffidently suggested by Crampton, which Hinton elevated to ordinal status. Nor is it the case, as Hinton supposes, that the eleventh abdominal segment of adult female

Boreus differs from that of other Mecoptera by lacking cerci; Byers (1961) showed their presence in *B. brevicaudus,* and I confirm their presence in *B. notoperates* as well. As Hepburn (1970) has already said, attempts to remove Boreidae to an order separate from the Mecoptera seems unjustified at this time.

Pupa

The metamorphosis to the pupa occurs in mid-August and in September in *B. notoperates* as in the other *Boreus* for which pupation has been recorded. Its onset is first recognizable by a separation, elongation, hypertrophy and migration of the pigment of the larval eye. The pigment becomes aligned and compacted as three nodes which, at 20°C, over a period of a week or more, move as a unit posteriorly and obliquely to the orbital region of the head (figs. 3F–I). For most of this period the larval jaws are functional, although feeding does not occur, and the larva moves about readily if disturbed.

During migration of the pigment, the purplish compound eye develops as though its posterior edge, defined by the three nodes of black pigment, were its developmental origin of growth. By the time that the imaginal eye is nearly fully outlined (fig. 3I), the larval-pupal apolysis has been completed, and the pharate pupa no longer can move the larval mandibles. Evidently this remarkable sequence occurs in at least some beetles as well. The migration of the pigment of the larval eye to the rear of the head in *Duvalius mallaszi* subsp. *chappuisi* Jean., described and figured from preserved specimens by the puzzled Jeannel (1926), is certainly an example of the same phenomenon; his specimens in which the pigment had separated from the stemmata are clearly pharate pupae.

It is during the migration of the components of the developing pupal eye that spermatogenesis occurs in *B. brumalis* (Cooper 1940) and *B. nivoriundus,* and not in the last instar larva as I stated earlier. In *B. notoperates,* however, only spermatogonial divisions and early prophase stages of the first meiotic division occur in the pharate pupa, the meiotic divisions and spermiogenesis taking place in the late pupa and pharate adult.

Within one to several days following apolysis, the larval-pupal ecdysis ensues. Initially the pupa, in contrast to the greasy-yellow, late pharate pupa, is a translucent white with the tips of the mandibles brown, and the eyes a purplish brown. Within a week the body

yellows, the moveable mandibles become testaceous to their bases, the eyes brown, yet with the three contrasting black nodes at their caudal margins distinct, and ocelli purplish, the malpighian tubules brown, and the bristles amber-brown. Within two weeks the eyes have become black, the three pigment nodes are still discernible, the ocelli are dark sepia, and the malpighian tubules are a dark purplish-brown. At five weeks the jaws and body are still moveable, but the pupal-adult apolysis has occurred. It is interesting that in the pharate adult female, the heavy black fixed setae of the gonapophyses attenuate near their midpoints; their threadlike prolongations (which are lost at ecdysis) connect with the corresponding setae of the pupal cuticle (fig. 3J). The pharate adult stage, during which the entire body, wings and legs of the imago darken, may last from ten days to three weeks. The pupal to adult ecdysis thus takes place (in the laboratory) from a month and a half to nearly two months after the onset of pupation. Unlike *B. hyemalis* (Withycomb 1922, Fraser 1943, Strübing 1950) and *B. westwoodi* (Brauer 1857, 1863), in which the newly eclosed adult requires from a number of days to as much as a week to reach full color, but like *B. brumalis* (Williams 1916), *B. notoperates* is fully colored within a half day following eclosion. Just how long the true pupal and adult stages last in other *Boreus* is not known. Until Hinton (1971, 1973) straightened out the matter, and called attention to it, the importance of dating the stages from their apolyses, rather than from their ecdyses, had not been appreciated. Strübing (1950, 1958) gives a duration for the "pupa" of *B. hyemalis* (as from) 40 to 59 days.

Habitat

The larvae and pupae of *B. notoperates* are found in the sods of mosses growing on diorite boulders from moderate (2 ft. dia.) to gigantic size. The immature stages occur in a very scattered distribution, and I have not been able to forecast, when the moss is of an appropriate species, whether or not a given moss-covered boulder will be found to be inhabited by *Boreus*. Ordinarily specimens are few amid the moss of a given boulder but, when found, tend to be clustered.

Initially I was unable to find immatures in the dry summer months. Because the mosses and their sods are very compact, desiccated and crumbly at that time, and frequently at a temperature (when sunned) of 30°C or more, it seemed likely that, following

melting of the snow, the young stages were washed to the ground, thereafter burrowing into the soil. Following that, they would forage as saprophiles, since Withycombe (1922) has found that larvae can feed on leaf mold. Promising moss-covered boulders, standing on a loose, fine and sandy soil, were therefore trenched on the run-off side to a depth of a foot or more, and the soil carefully sifted through Tyler screens down to 16 meshes to the inch (0.99 mm openings). This seemed a hopeful attack at the time because Strübing (1950) had found that *B. hyemalis,* during periods of drought, descend to a depth of as much as 20 cm below their mosses, which grow on soil, to reach a suitably humid surrounding. No *Boreus* were found.

During one collecting period in mid-August there was a brief but heavy shower which, within 20 minutes, brought the mosses on the boulders to a fresh, expanded green state, and soaked their sods through. When the damp sods were broken or sliced open, there amid the rhizoids were the larvae and pupae within small ellipsoidal and cylindrical spaces that had readily cleaved open! During dry periods these cells, which are only slightly larger than the stages enclosed, harden and act thereafter as a coherent whole, appearing as no more than larger, compact particles of the sandy soil and organic debris of the desiccated sod. When such sods are broken and crumbled, these cells remain intact, even under the stresses of sifting. Their inner walls are very smooth, and are perhaps cemented by salivary secretions, but not by silken threads as has been suspected or claimed for the pupal chambers of *B. westwoodi* (Brauer 1863) and *B. hyemalis* (Withycombe 1922, Syms 1934). It is possible that salivary secretions also make their walls impervious to water loss. Thereafter search became routine during the predominantly dry periods for the desiccated mosses on their boulders need only to be soaked with water.

It is clear that *B. notoperates* is well adapted by its earthen chamber for survival during periods of drought. The larva must do most of its foraging during the spring before the moss turfs become dry, and thereafter as infrequent opportunity permits following scattered storms on the mountain.

Associated Mosses

Records of the mosses with which *Boreus* is associated in one way or another have been made for only seven or eight of the twenty-seven or so species of *Boreus* known (species list in Svensson 1972),

and for but four species are the mosses known upon which the larvae feed. I shall bring these records together and discuss them at another time. Suffice it to say that more than forty species of moss are involved, and that these are distributed among 9 orders, 19 families, and 28 genera. The families of mosses for which a member (or members) is known to support the life history of a species of *Boreus* are Dicranaceae, Bryaceae, Mniaceae, Thuidaceae, and Polytrichaceae. Records which follow for *B. notoperates* now add two additional families: Grimmiaceae and Orthotrichaceae. The generic and specific names are those recognized by Crum, Steere and Anderson (1973).

B. notoperates uses as food and habitat for its larval stages: *Grimmia apocarpa* Hedw., *G. montana* B.S.G., *Rhacomitrium sudeticum* (Funck.) B.S.G., and *Orthotrichum rupestre* Schleich. *ex* Schwaeger. Each is widely distributed, being found in Europe, Asia, and North America. Adults have been collected on all of the above, as well as on the following: *Grimmia laevigata* (Brid.) Brid.; *Tortula princeps* De Not. and *T. ruralis* (Hedw.) Gaertner (Pottiaceae); *Homalothecium aeneum* (Mitt.) Lawt., *H. nevadense* (Lesq.) Ren. & Card., *H. pinnatifidum* (Sull. *et* Lesq.) Lawt., and *Camptothecium amesiae* Ren. & Card. (all Thuidaceae). The identifications of all of these mosses have been made by Professor Lewis E. Anderson of the Department of Botany, Duke University, Durham, N.C., and voucher specimens have been retained in the herbarium at Duke University.

Adult *B. notoperates* will browse in the laboratory on all of the mosses listed above. But of the mosses upon which only adults have been collected, only *Grimmia laevigata* and the two species of *Tortula* are widely distributed (Eur., Asia, N. A.), and by the nature of their rhizoids and sods are likely candidates as larval habitats and food. The sods of the mosses in which larval and pupal *B. notoperates* have been found are compact, but surprisingly thin, falling within the range from 5–10 mm when dry, and from nearly 6–12 mm when thoroughly damp. The Thuidaceae, on the other hand, are all endemic species. Because their clumps are coarse, open, and generally without a suitably fine rhizoid mat and sod, they are probably not used as larval habitat and food mosses.

It is of particular interest that the mosses which serve as larval food for *B. notoperates* are very widespread; also that *B. notoperates* is not limited to a single species or genus of moss but in fact utilizes members of two families representing different orders (Grimmiales and Isobryales). Whatever limits the geographic distribution

of *B. notoperates,* it is certainly not the availability of a local or special moss. That generalization holds as well for those other species of *Boreus* for which associations with mosses have been specifically recorded; nearly all of the mosses concerned are widespread in Europe, Asia and North America, and indeed quite a number have a still more extensive range than that.

Variation Among Adults

When *B. notoperates* was described (Cooper 1972), my series of 29 specimens was nearly uniform with respect to antennal joint number, namely 19 joints — a feature used as a specific character. The only apparent exceptions that I noted I did not take to be such; they were a male and female, each of which had an incomplete separation of joints-3 from 4, but these joints were otherwise demarcated by their apical swellings. Since then I have found that individuals do occur with antennal joint numbers other than 19–19.

In a series of 86 males and 83 females held to determine their relative lengths of life in the laboratory ($\bar{m}♂ = 16$ days, $\bar{m}♀ = 22$ days; $0.05 > P > 0.02$), the distributions of antennal joint numbers were:

	18–18	18–19	19–19	19–20	20–20	Total
♂ ♂	12	4	68	1	1	86
♀ ♀	9	3	70	0	1	83

Thus about 12% of *B. notoperates* have a different antennal joint number than 19–19. When numbers of 19–19 individuals are compared with the lumped totals of the others, there is no evident difference between male and female ($0.8 > P > 0.7$). Males with antennal joints fewer than 19–19 do tend to die somewhat earlier than the other males ($\bar{m} = 11$ days), the Wilcoxon rank sum test giving $0.02 > P > 0.01$. Such females also die somewhat earlier ($\bar{m} = 19$ days), but not significantly so, for $0.5 > P > 0.4$.

Attention is also called to new information on patterns of abdominal fusions in males (Cooper 1973).

Predators, Parasites and Life Cycle

Very little has been recorded regarding the use of *Boreus* as prey. Withycombe (1922) was of the opinion that the adult would be expected "to be speedily devoured" by birds, unless distasteful. Greve

(196) holds *Boreus* to be acceptable to small birds as welcome supplement to their winter fare, and that *Boreus'* escape leap and thanotaxis perhaps offer it some protection against predation. No one seems to have observed birds feeding on *Boreus,* however, and McAtee's extensive analysis of the stomach contents of birds provides no records. Lestage (1940), on the other hand, cites a unique record of the remains of *Boreus* from the stomachs of trout, even adding "[les] Truites ont montré celles-ci friandes des Boreus"! Other possible predators that have been mentioned are spiders, often abundant on snow during warmer days, and rapacious insects (Vlasov 1950, Greve 1966) — but none have been shown to be such. Definite information, however, can be given on actual and probable parasites of species of *Boreus.*

In my own experience, I have but once found mites on *Boreus.* Four adult individuals of a species of *Pediculaster* (Pyemotidae; determined by Prof. Earle A. Cross) were in neat parallel array, lengthwise to abdominal sternites-1 and 2, nearly concealed between the abdomen and the dorsal faces of the metacoxae, on which they were seated, of an adult male of *B. brumalis* (Hanover, N. H., Jan. 8, 1961, air temp. 1.7°C). The record is of special interest for it is a likely, occasional parasite of *Boreus.* Insofar as the habits of species of *Pediculaster* are known, they are ordinarily phoretic on a number of diverse flies, and Vitzthum found that *P. mesembrinae* (Canestrini) drop off their hosts at oviposition sites, attacking there the developing fly larvae (see Cross 1965).

A not surprising second parasite of *Boreus* is a *Cordyceps* (Sphaeriales, Clavicipitaceae) that in one case of 5 such emerged from the intersection of the frontal and coronal sutures, as well as from between the 9th and 10th abdominal tergites of a mummified 4th instar larva of *B. brumalis* found erect in its vertical burrow just beneath the basal stems of the host moss, *Dicranella heteromalla* (Hedw.) Schimp. (Princeton, N.J., Nov. 19, 1939). The portion of the fungus from the head bifurcated into two fruiting bodies (each about 3–4 mm long), extending vertically upwards and nearly parallel. The limb from the abdomen bent sharply and vertically upwards, and was nearly 5 mm long. In all, the 5 *Cordyceps*-infected larvae were among 25+ larvae collected that day from one large turf of the moss growing at the base of a tulip tree. Of 35 pupae collected at the same site and time, none were afflicted by the fungus.

The only parasites that have been recorded from *B. hyemalis* are hymenopterous. The braconid *Dyscoletes lancifer* Haliday was shown

by Aubrook (1939) and Fraser (1943) to be a parasite of the larva. Withycombe (1922) had earlier reported hymenopterous parasites of the larva, but it is by no means certain that they were also *Dyscoletes*. Indeed, of the single larval parasite that Withycombe endeavored to rear, but which was destroyed by mold as a pupa, he says that it appeared to be that of an apterous form. At Princeton, N. J., I too obtained hymenopterous larvae from larval *B. brumalis* in the autumn, but was unable to rear them.

From 13 *B. notoperates* larvae collected at Coldwater Canyon on Mt. San Jacinto (Aug. 22, 1973), 17 hymenopterous larvae emerged (3 from 1 larva, 2 from each of 3 larvae, and 1 from each of 8 larvae); one additional larva was obtained from a larval cell of *Boreus* containing the remains of the mecopterous larva. By February 1, 1974, only 5 specimens (4♀, 1♂) had transformed to adults. All are a megaspilid (Ceraphronoidea), and are tentatively identified as an undescribed species of *Conostigmus*.[12] It is an interesting association, for so far as I am aware no ceraphronoid is known to have a mecopterous host, although there are records of neuropteroid hosts (*e.g.*, Muesebeck 1959, Dessart 1967).

Withycombe (1922), who thought — like many others — that *Boreus* has an annual cycle, was puzzled as to what alternative host a hymenopterous parasite of *Boreus* might attack from August to December. This, so that it could have a brood appearing early in the new year that could once again parasitize a new generation of *Boreus*. Syms (1934) and Aubrook (1939), however, conclude from their finding in the autumn, of two stages of the larva of *B. hyemalis*, that *Boreus* probably has a 2-year life cycle, and Syms actually showed this to be so for at least some larvae. That it does in fact have a 2-year cycle has been proven conclusively by Strübing (1950), and it is very likely that all *Boreus* have a cycle that normally takes 2 years — assuredly that is so for *B. notoperates*, *B. brumalis*, and *B. nivoriundus*, which I have studied. The problem that Withycombe posed thus vanishes, for the larvae of a second generation of *Boreus* are available at any time that the hymenopterous parasite emerges and is ready to oviposit. Such parasites of *Boreus*, therefore, *could* be specific parasites, having no other host.

In the case of the larva of *B. notoperates*, confined as it is to hard earthen cells for perhaps half of its life, it is likely that the parasite

[12]Dr. Paul Dessart, Chef de Travaux, Entomologie, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, has very kindly confirmed the generic placement of *Conostigmus* (March 11, 1974).

can attack its host only during periods of dampness when the larva of *Boreus* is free to move about; since the parasite pupates, or may enter diapause, enclosed within the cell of its host larva, parasite and host are thereby synchronized to the same periods of activity. The very means by which the larvae of *B. notoperates* withstands drought thus entrains the parasite to the host's timetable.

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EMERGENCE PATTERNS OF THE SUBALPINE DRAGONFLY *SOMATOCHLORA SEMICIRCULARIS* (ODONATA: CORDULIIDAE)

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Introduction

The genus *Somatochlora* is circumpolar and many of its species reach high into the subarctic and subalpine regions. *S. semicircularis* occurs in the Canadian and Hudsonian zones of the North American Western Cordillera from Alaska to Colorado. Towards the southern part of its range, this species is found at high altitudes in Colorado where adults have been recorded at 3000 to 3700 m (Gloyd, 1939; Walker, 1925; Carpenter, 1873). Larval habitats range from 2700 to 3600 m in shallow ponds and water meadows. These may well be the highest breeding localities for any odonate known.

The alpine and subalpine habitats offer extremes in temperature and insolation during the short growing season which follows the late snow melt (Mani, 1968). The subalpine regions, particularly, present relatively the highest day and lowest night temperatures (Billings and Mooney, 1968). Coupled with these factors, the frequent periods of drought and general unpredictability of climate contribute to the rigor of the high altitude habitat. Studies of life history strategies of insects which have adapted to high altitudes have revealed cold resistance and lowered temperature thresholds, a predominance of diurnal activity, a seasonal delay and shortening of the flight period, and a general increase in the length of the life cycle coupled with overwinter hibernation or diapause (Mani, 1968). In the dragonflies, the increased life cycle is accomplished by elongating the larval period to as much as three or four years (Paulson and Jenner, 1971; Robert, 1958). *Somatochlora semicircularis* larvae are also resistant to dessication when their ponds and water meadows dry up annually (Willey and Eiler, 1972). An ecologically sensitive part of the life history for a dragonfly is the emergence period during which the "aquatic" larva leaves the water, transforms into the

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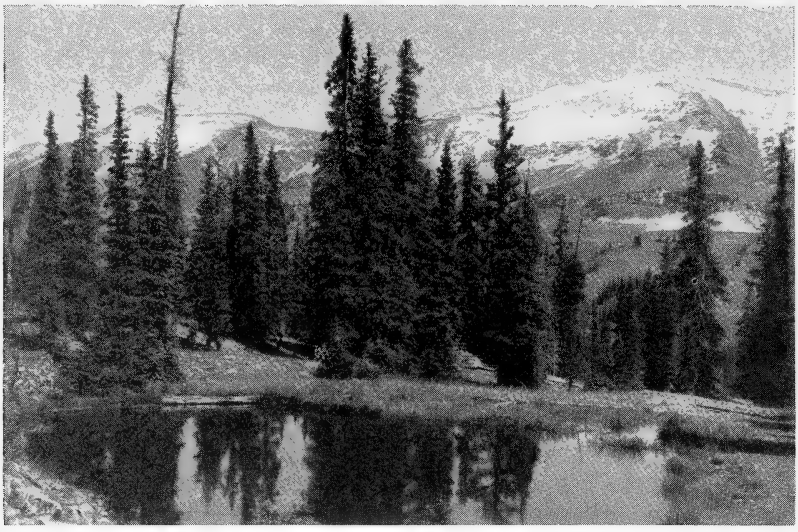

Figure 1. Pond Nine (3416 m) on Galena Mtn. in the Mexican Cut Research Area owned by The Nature Conservancy. 7 September 1970.

winged adult, and flies away as a reproductively immature (teneral) adult. The observations reported here are intended to correlate a late emergence season, a possible lowered temperature threshold, a complete shift to diurnal behavior, and an abbreviated, synchronized emergence period with the rigors of the high altitude habitat in Colorado.

Habitat

Two subalpine ponds were selected for study areas. They represent the typical habitat where larvae of *Somatochlora semicircularis* are found. The emergence areas of both ponds are restricted to the shallow, sedge-filled margins.

Pond Nine (3416 m) is one of a group of small ponds in the Mexican Cut Research Area on Galena Mountain (Gunnison Co., Colorado) owned by The Nature Conservancy and administered by the Rocky Mountain Biological Laboratory. It is 10 m in diameter and 1 m deep in the center. About 50% of its shoreline is lined with *Carex rostrata* and *C. aquatilis* in the shallow bays which make up the emergence areas for the dragonflies. The center of the pond is

lined with *Isoetes bolanderi* on the bottom. The pond is surrounded by a belt of forb-sedge meadow which is surrounded by an open association of spruce-fir (*Picea engelmanni* and *Abies lasiocarpa*) (Fig. 1). In the past eleven years of observation, Pond Nine has never totally dried up.

Irwin Pond South (3141 m) lies near the edge of Lake Irwin (Lake Brennan) near Kebler Pass in Gunnison Co., Colorado. Its basin is 45 m in diameter, 1.2 m deep in June and dries up in late August and early September (observed 1968-1973). The shoreline and shallow areas where emergence takes place are lined with *C. rostrata* and *C. aquatilis*. The deeper areas support *Potamogeton foliosus* and *P. illinoisensis* and thin mats of *Drepanocladus uncinatus*. This pond has been described further by Willey and Eiler (1972).

Materials and Methods

The emergence of *Somatochlora semicircularis* was studied from 1968 to 1972. At first, the transforming larvae were marked by surveyor's flags so that the transformation of each individual could be accurately timed. Considerable trampling of the habitat was unavoidable so that the studies were repeated in 1971 by making daily collections of the cast skins left behind by the teneral adults. Fewer larvae were damaged during their transformation by this method. However, more larvae were lost through bird predation so that their cast skins could not be recorded. In order to verify the diurnal pattern of the teneral flight in an undisturbed habitat, continual observations by binoculars of the ponds were conducted from 100 feet away from the shoreline in 1972 during the peak of the emergence period.

Water temperatures were measured 3 cm below the water surface in areas of highest emergence activity. Solar radiation was measured by a recording Belfort pyrheliograph with a 12-hour gear. Environmental air temperatures were measured with a YSI telethermometer shielded from radiation by thin, flat, double-layered shields, 46 cm square, which were set horizontally 8 cm above and below the temperature probe. The inner surface of each was painted flat black and the outer surface was glossy white (Platt and Griffiths, 1964).

Observations

About one month after the ice leaves the ponds, the first larvae of *S. semicircularis* leave the water, undergo transformation, and fly

Table 1. The annual emergence periods for *S. semicircularis*

Location	Year	1st day of emergence	Total adults	Emergence Total days	Days until 50% emergence
Pond Nine	1968	15 July	543	14	3
	1969	7 July	166	15	3
Irwin Pond S.	1971	3 July	1528	21	6

away from the ponds as teneral adults (maiden flight). At Pond Nine, emergence began on 15 July 1968, 7 July 1969, and 6 July 1970. At Irwin Pond South, slightly lower in altitude and more sheltered by spruce-fir, emergence began slightly earlier — 30 June 1970, 3 July 1971, and 27 June 1972.

The total period during which emergence occurs each year is short (Table 1). The total annual production of adults occurs over an average of 16 days during which 50% of the adults emerge within the first three to six days. The 1969 emergence curve (Fig. 2) demonstrates a typical, highly synchronized pattern. The 1968 curve (Fig. 3) shows the effect of stormy weather and low temperatures on 17 and 18 July which delayed the emergence of some of the larvae and extended the emergence period. No secondary peak of emergence was ever observed later in either season.

The distance flown during the initial flight of the teneral adults is unknown. However, they remain away from the ponds, presumably in the forest near the ponds or at lower altitudes, for one to two weeks. In 1968, the first tenerals left Pond Nine on 15 July and the first mature males were observed patrolling the edges of the pond on 22 July — 7 days later. By this time, 95% of the adults had emerged and flown away (Fig. 3). In 1969, the first tenerals left on 7 July and the first patrolling male was sighted on 22 July — 2 days after the last teneral adult had flown (Fig. 2). These mature adults are individuals which emerged at the beginning of the emergence period, have matured, and returned to the pond for mating. Teneral adults and reproductively mature adults are considered here to be all part of the same emerging population. They are just temporally separated. On two occasions mature males were observed patrolling a pond when a newly emerged teneral flew up from the sedges on its maiden flight. On both occasions, the mature male harassed and tried to couple with the soft teneral before the latter could leave the pond. One of the tenerals was probably injured by

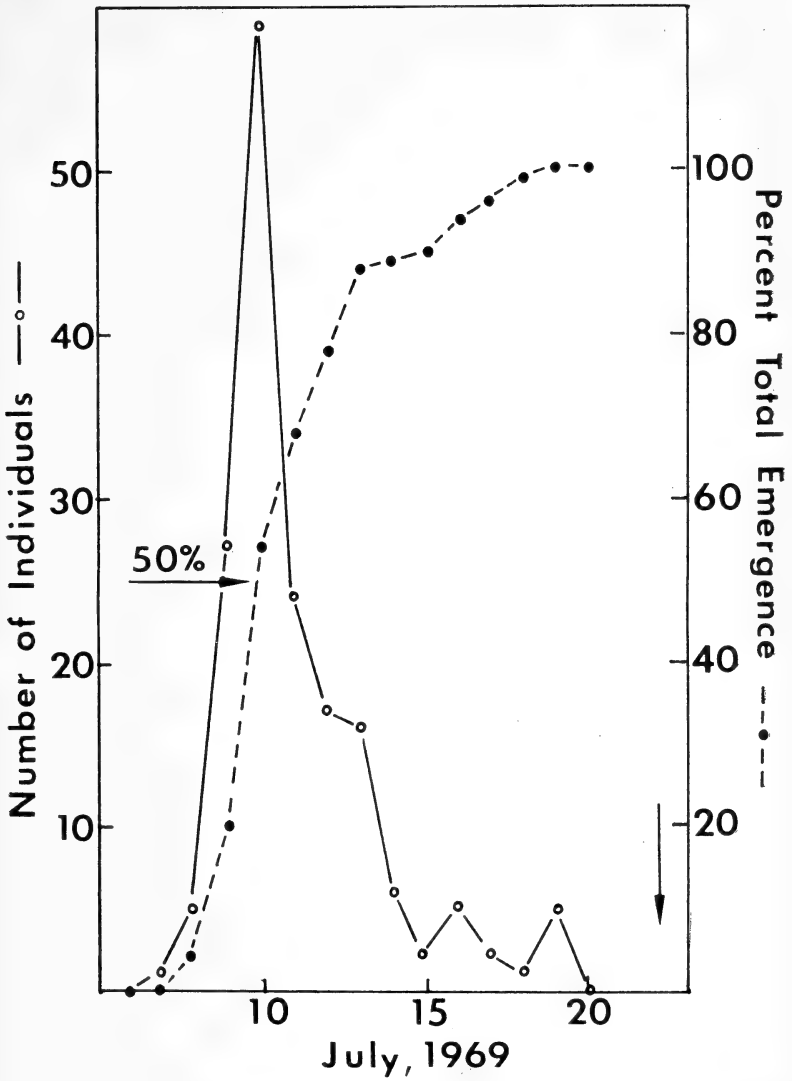

Figure 2. Seasonal emergence pattern of *S. semicircularis* at Pond Nine, 1969. Vertical arrow marks day on which first reproductive male was observed patrolling the pond.

the encounter because its subsequent flight was very erratic. The *Somatochlora* males are very aggressive and will try to grasp any other dragonfly — its own species, *Cordulia shurtleffi*,[1] or even the much larger *Aeschna interrupta*.

Water and air temperatures are relatively low in ponds at high altitudes although the diurnal water temperatures are not as low as might be expected due to the heat absorbing qualities of the pond bottoms and the shallowness of the water. The water temperature averages 12°C. (varies from 9° to 14°C.) when the larvae first emerge in the morning, whereas the air temperatures, which rise very rapidly once the sun is up, average 9°C. (vary from 4° to 12°C.). The night air temperatures drop below freezing and, on many mornings, frost still lay on the ground when the first larvae appeared. The larvae climb up the sedges in areas where the water is seldom more than 30 cm deep and usually 3 to 8 cm deep. The larvae start to leave the water after sunrise (0700 to 0800 MDT).

The maximum number of larvae leave the water between 0800 and 1100 hours (Fig. 4). By 1000 to 1700, they are ready to fly. In 1972, observations of undisturbed ponds indicate that 75% or more of the tenerals actually leave the ponds between 1100 tnd 1230 if the weather is fair and the air temperature varies between 16° and 18°C. The initiation of the flights appears to be temperature-dependent. On 1 July 1972, flights began at 1100 with an air temperature of 18°C. The flights stopped abruptly at 1230 when clouds covered the sun and the air temperature dropped to 14°C. Flights did not resume until 1430 when the sunshine returned and the air temperature rose to 16°C. All flights ended for the day at 1500 when a thunderstorm started and the air temperature dropped to 14°C. and below. Any adults which had not flown by this time had to remain on the sedges until the following morning.

Birds are the main predators of *Somatochlora* during the actual transformation process. Spiders and ants will attack larvae near the shore but generally account for a very small proportion of the loss. Specific data are being assembled for a separate report on bird predation and will not be presented here. However, a general summary is essential for the present argument. In general, bird predation does not begin until the second or third day of emergence. Under normal weather conditions, daily loss does not exceed 30 to 50% of the

[1]In the studies on drought resistance in *Somatochlora* larvae, Willey and Eiler (1972) misidentified *Cordulia shurtleffi* larvae for those of *Libellula quadrimaculata*.

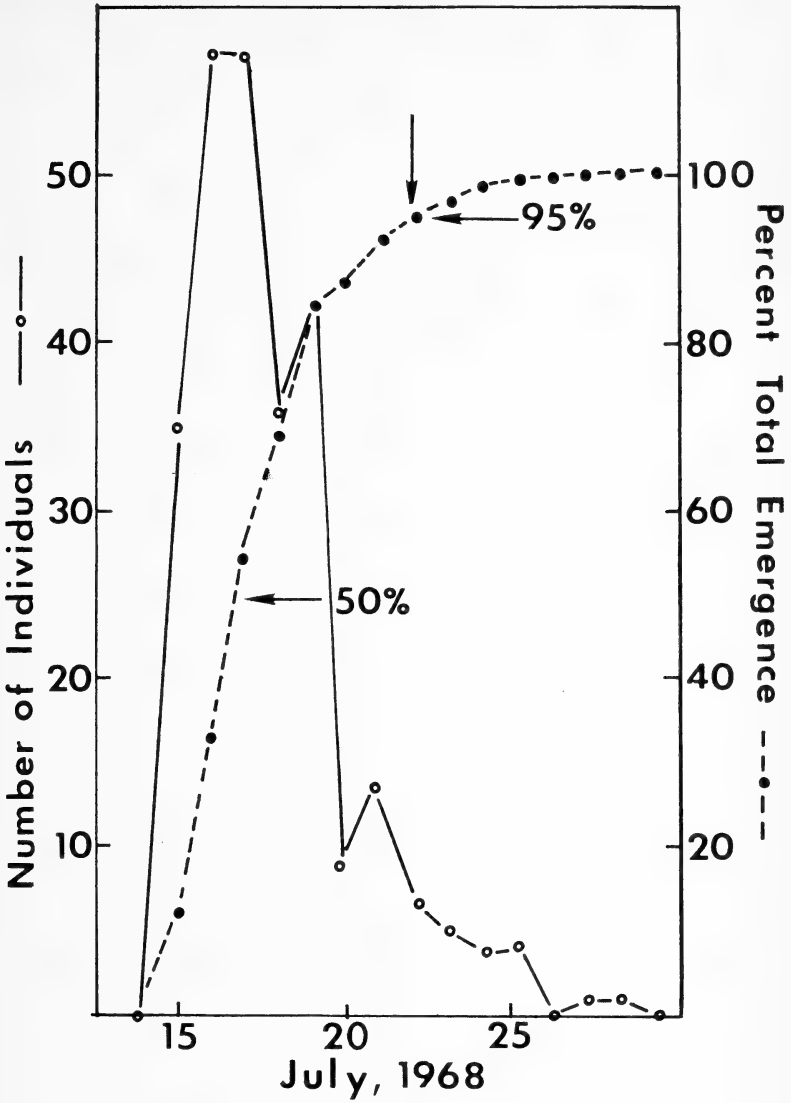

Figure 3. Seasonal emergence pattern of *S. semicircularis* at Pond Nine, 1968. Vertical arrow marks day on which first reproductive male was observed patrolling the pond.

dragonflies until the second week of emergence. On cold and stormy days, loss may approach 100% at any time during emergence. Adults which have transformed but have been prevented from flying by low temperatures or rainy weather may remain clinging to the sedges for a day or more. Most of these adults fall prey to birds. Once the tenerals fly, they are reasonably free from bird predation. Only one teneral has been observed to be caught by a bird (Western flycatcher) during its maiden flight.

Discussion

Somatochlora semicircularis is a western cordilleran dragonfly whose adults normally appear between the middle of June and the middle of July (Walker, 1925). The Colorado ponds under investigation occur at the southern limit of the species and yet the adults emerge in early July and appear as reproductives in mid-July near the end of the general emergence season. Such a relatively late season is probably correlated with the late snow melt and low temperatures of its high altitude habitat. Schiemenz (1952) has reported a similar delay of season correlated with altitude for *Libellula quadrimaculata.*

Dragonfly emergence has been shown to be temperature-dependent with the initiation of emergence primarily dependent on water temperature (Trottier, 1973; Corbet, 1963). The larvae of *S. semicircularis* in Colorado first leave the water when the water temperatures average 12°C. and the air temperatures average 9°C. Comparative data for other corduliid dragonflies are not available. The only data available come from the studies of the aeschnid dragonfly *Anax.* Corbet (1957) found that *A. imperator* in England normally left the water when the temperature reached 19° to 22°C. (air temperature, 12° to 15°C.). Trottier (1973) found that *A. junius* in Ontario, Canada, normally initiated emergence when the water temperature reached 24°C. (air temperature, 15° to 20°C.). At water temperatures below 17°C., the *Anax* larvae which had left the water would return to the water and delay emergence until the following day. The *Somatochlora* larvae were able to leave the water and undergo transformation at average temperatures 5°C. below the minimum for *Anax* larvae. Whether this difference is a specialization to high altitudes or is only a general family difference must be further investigated.

In general, teneral corduliid dragonflies at lower altitudes and/or latitudes are ready to fly early in the morning. However, the emer-

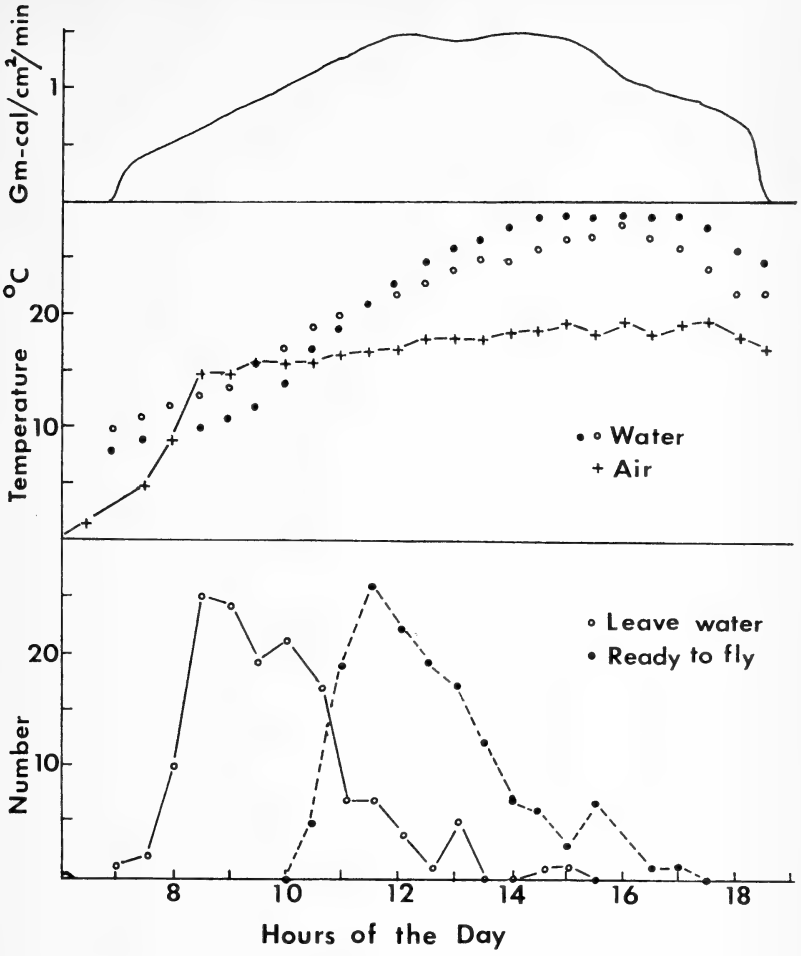

Figure 4. Daily emergence pattern of *S. semicircularis* on 2 July 1970 at Irwin Pond South. Lower curve shows the number of nymphs leaving the water (solid line) and transformed teneral adults ready to fly (dashed line) at successive hours during the day. Middle curve shows water temperature 3 cm below the surface at two separate stations, 1 m apart, and air temperature 45 cm above the surface of the water in the emergence area. Top curve shows solar radiation. Nymphs recorded here completed the entire transformation process successfully.

gence pattern is variable and freshly emerged adults have been collected throughout the day and even in early evening on cold, cloudy, or rainy days (Lutz and McMahan, 1973; Corbet, 1963; Lutz, 1961; Taketo, 1960; Kormondy, 1959; Robert, 1958; Lieftinck, 1932). The larvae of *S. semicircularis,* under normal conditions, do not leave the water until after sunrise and the tenerals generally fly at noon. A similar shift of the emergence pattern to the middle of the day has been described for *Aeschna interrupta* at high altitudes in California (Kennedy, 1925) and for *Aeschna subarctica* on the moors near Kiel, Germany (Schmidt, 1968).

The emergence curve of *Somatochlora* in Colorado is characterized by brevity (16 days) and a high degree of synchrony (Fig. 2, Table 1). Similar synchrony has been described for other dragonfly species which have been categorized by Corbet (1963) as "spring" species. Only one of these species, *Oplonaeschna armata,* exhibits a shorter time for the total period (10 days) and for the 50% emergence time (2 days). *Oplonaeschna* inhabits the water-pocket streams of New Mexico and Arizona and is subject to flash floods and severe dessication (Johnson, 1968). The lower altitude corduliid, *Tetragoneuria cynosura,* averages a 23-25 day emergence period with 50% of the adults emerging by the 6th or 7th day in Michigan (Kormondy, 1959) and North Carolina (Lutz and McMahan, 1973; Lutz, 1961 and 1962). *Tetragoneuria* in Michigan also exhibits a bimodal curve in which a second peak of emergence occurs 10 days after the end of the first peak. This bimodality has been described for other dragonfly species (see Corbet, 1963) but is missing in the *Somatochlora* curve (Figs. 2 and 3).

Selective pressures contributing to the synchrony of the single peak of the *Somatochlora* emergence curve may well involve the brevity of the season. Both in 1968 and 1969, 10 days after the end of the initial emergence peak at a time when *T. cynosura* (Kormondy, 1959) and *Anax imperator* (Corbet, 1957) normally exhibit a small second peak of emergence, the shallow areas at Irwin Pond South and Pond Nine had largely dried up. *Somatochlora* larvae leave the water by climbing up the emergent sedges. They do not crawl out on the land. Lack of emergence sites or competition for the few remaining sites can be expected to be a factor in selecting for a temporal shift toward early emergence.

Another contributing factor may involve intraspecific interference. The diurnal emergence pattern which is necessitated by the climatic character of the habitat creates problems which normally do not affect

nocturnal or early morning emerging populations. Teneral adults which fly up during the middle of the day are subject to harassment and possible damage from the reproductive males. However, by the time the first *Somatochlora* reproductives return to the Colorado ponds, 95 to 100% of the annual production of tenerals have already left the pond (Figs. 2 and 3). The diurnally temporal separation of the reproductives and the nocturnal or early morning tenerals of the lower altitudes has been replaced by the seasonal separation of a 1 to 2 week teneral maturation period during which time the dragonflies fly in the forest away from the ponds while the remainder of the population is emerging. The high altitude ponds of Colorado seem to be sufficiently isolated from each other to keep recruitment of reproductives from lower, and therefore earlier, ponds to a minimum.

The diurnally transforming dragonflies are also exposed to predation by birds. The highly synchronized emergence of *Somatochlora,* however, provides that the relatively large number of larvae which emerge during the first few days ensure that many tenerals get away from the pond. To what extent a synchrony of emergence provides selective advantage to the dragonfly population by (1) partially forestalling the results of a revised predator searching image and/or shift in prey preference or (2) saturating the environment with prey with a resulting early satiation of the predators is as yet undetermined. It is likely that both predation tactics are involved and thwarted by this mechanism.

Summary

Somatochlora semicircularis has been able to adapt to the rigors of the subalpine and lower alpine habitats of Colorado. The corduliid tendency toward a flexible, early morning emergence pattern has contributed to its shift to a full diurnal emergence pattern. In addition, it may be able to initiate emergence at relatively low water and air temperatures. The emergence pattern has been strongly synchronized, shortened and restricted to a single seasonal peak, possibly as a result of ponds drying up early in the season at high altitudes, predation pressure, which may be the same or worse than that at lower altitudes, and the effects of potential interference between the aggressive reproductive males and the soft-cuticled teneral adults.

Acknowledgements

I wish to thank Dr. Robert B. Willey for constant advice and encouragement. I appreciate the valuable critical reviews by Drs.

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THE MILLIPED GENUS *BOLLMANELLA* (DIPLOPODA, CHORDEUMIDA, CONOTYLIDAE)

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Even while my recent (1970) revision of the milliped Family Conotylidae was in press, new data on the family had begun to accumulate. This paper is the first of a series of supplemental reports designed to update our knowledge of the conotylids, a group of millipeds of considerable importance in biogeography.

Like many other milliped genera and species, the genus *Bollmanella,* and its single species *B. oregona,* have remained enigmatic since they were described from a single male specimen by R. V. Chamberlin in 1941. The description of the genus alluded mostly to body form and color, and even contradicted the specific diagnosis of the only included species. The description of *B. oregona* also contained errors, and no illustrations were provided. As if this were not enough, the type locality suggested an error of several hundred miles.

The type of *B. oregona* was in the Chamberlin collection in Salt Lake City. The diplopod portion of the collection has remained uncurated since Chamberlin's death and is in a confused state, but while my conotylid revision was in press, Mr. Thomas Lorenz, then in charge of the collection, found the holotype of *B. oregona* and loaned it to me.

In 1973, I was fortunate in receiving a large number of Berlese extraction samples from Mrs. Ellen Benedict, Portland State University, Portland, Oregon, and from Dr. David Malcolm, Pacific University, Forest Grove, Oregon. These samples were rich in millipeds of many groups previously known only from a very few specimens, and included literally hundreds of individuals of the related genera *Taiyutyla* and *Bollmanella.* Members of these genera must be among the more common humus animals in the area of coastal Oregon. As I mentioned earlier in reporting on part of these collections (Shear, 1973), northern California and the state of Washington are much in need of the kind of thorough exploration by

[1]Part of the work for this paper was done while a Richmond Fellow at Harvard University.
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Berlese extraction which Benedict and Malcolm have carried out in Oregon.

It is now possible to do a number of things about *Bollmanella,* which in 1970 I had to treat as a *nomen dubium.* 1) The genus can be characterized as fully distinct and valid, separate from, but related to, *Taiyutyla* and *Conotyla,* and more distant from *Austrotyla* and *Achemenides,* 2) some clear ideas of the distribution of the genus can be gained, and 3) seven new species can be described.

The distribution of the eight known species of *Bollmanella* ranges from southern coastal Oregon to just above the Columbia River in Mason Co., Washington, with one species reported here from the Wallowa Mountains in extreme northeastern Oregon. The scattered nature of the localities suggests that species of *Bollmanella,* except for *B. oregona,* have small ranges, and we might expect many more to be discovered. In particular, the isolated mountain ranges of eastern Oregon need exploration.

Ecologically, *Bollmanella* species have been collected exclusively from litter and duff derived from deciduous trees. Conifer duff and litter support species of *Taiyutyla,* though members of this latter genus are also found in deciduous duff, often syntopically with *Bollmanella* species. Although *B. oregona* ranges from sea level to around 2000′ elevation, most of the other species seem to have been collected from forests or parkland between 900′ and 1500′ elevation. This contrasts again with some species of *Taiyutyla,* which (unpublished data) are known from quite high elevations. Species of an unrelated chordeumid genus, *Rhiscosomides* (Shear, 1973), are found at low elevations and seem to favor coniferous forests. This ecological data also represents information from many collections which did not contain specimens of *Bollmanella,* thus clearly suggesting which habitats are most favorable.

All type specimens of new species have been deposited in the Museum of Comparative Zoology, Cambridge, Mass.

Superfamily Heterochordeumatoidea Pocock
Family Conotylidae Cook
Genus *Bollmanella* Chamberlin

Bollmanella **Chamberlin, 1941, Bull. Univ. Utah Biol. Ser. 6(5): 12. Type species, *B. oregona* Chamberlin, by monotypy and original designation.**

Diagnosis: With the characters of the family. Small (ca. 6-7 mm long) conotylid millipeds with typical form, distinct in gonopod morphology. Anterior gonopods simple, usually acuminate, but may

be apically laminate, or may bear a basal mesal branch. Anterior gonopod sternum bandlike and well-sclerotized. Posterior gonopods three-segmented, coxal segment with large, prominent colpocoxites characterized by a basal flagellar branch usually more or less sheathed by a development from the main part of the colpocoxite. Apical two segments typical for family. Posterior gonopod sternum with a T-shaped process between the coxae in most species. Third and fourth legpairs of males enlarged, strongly bowed, but with, at most, small mesal femoral knobs. Legpairs 5-7 either normal in size and form, or decreasing from slightly enlarged to normal in size. Prefemora of male legpair 11 with mesobasal processes. Female genitalia without any useful taxonomic characters.

Remarks: Bollmanella is clearly related to *Taiyutyla,* with which it is entirely sympatric, and often syntopic. However, the uniformly smaller size, the flagellar branch of the posterior gonopods, and the T-shaped process of the posterior gonopod sternum clearly set *Bollmanella* species apart as a distinct phyletic line.

I would like to comment further on the Family Conotylidae as a whole, but several factors preclude it at this time. The genus *Taiyutyla* remains to be revised, and is affected by, as are any conclusions about Conotylidae at this time, the description by Loomis and Schmitt (1971) of several extremely interesting new higher taxa related to conotylids, including new subfamilies and a new family. The *Taiyutyla* material I have examined so far will also enable me, in this projected future paper, to comment in detail on the functional aspects of the gonopod complex.

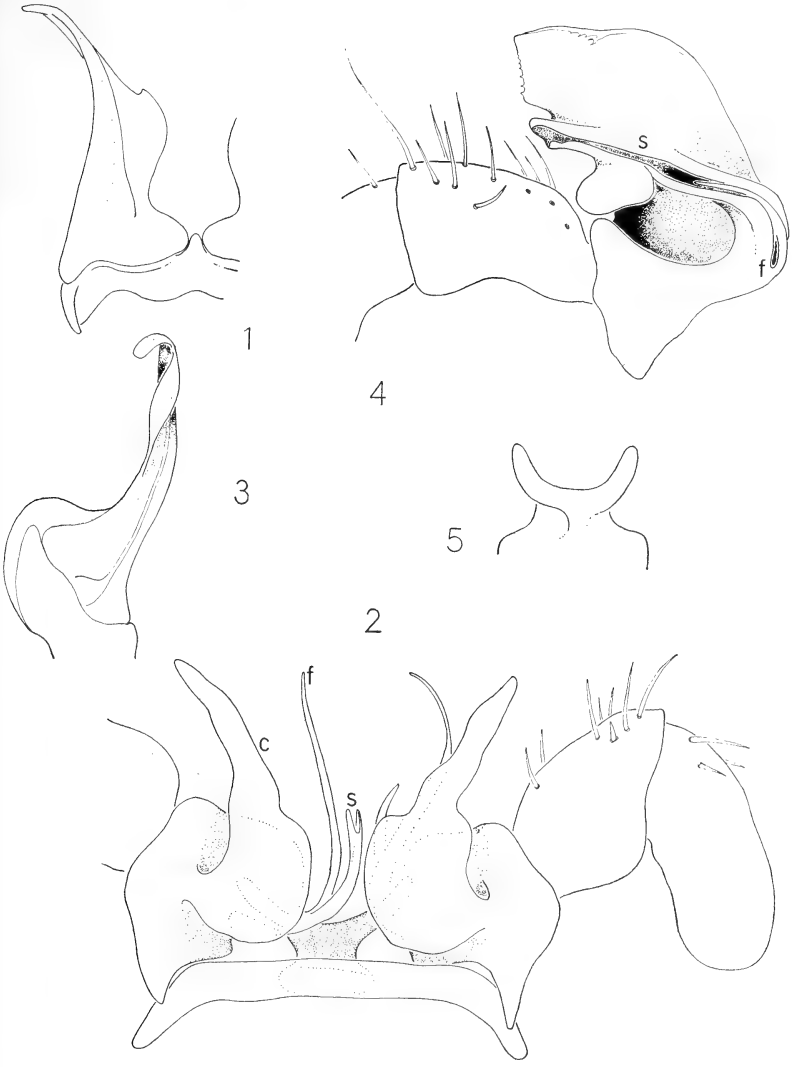
I am still unable to find any taxonomically useful characters that will allow reliable separation of females of the various species of conotylids, and members of *Bollmanella* are no exception. However, in the hope that some usable characters might turn up in the future, I have designated *bona fide* female paratypes where possible. I do not present a key to the eight known species, as they can readily be separated by reference to the illustrations of the gonopods. The gonopods of these species are so small they must be mounted on slides temporarily (in glycerine) to see detail.

Bollmanella oregona Chamberlin

Figs. 1, 2

Bollmanella oregona Chamberlin, 1941, Bull. Univ. Utah Biol. Ser. 6(5): 12, no illustrations.

Type: Male holotype from "John Day Creek," Douglas Co., Oregon, collected by J. C. Chamberlin, 19 November 1939. In



Figs. 1, 2. *Bollmanella oregona.* Fig. 1. Right anterior gonopod, posterior view. Fig. 2. Posterior gonopods, anterior view. Figs. 3, 4. *B. reducta.* Fig. 3. Left anterior gonopod, posterior view. Fig. 4. Right posterior gonopod, posterior view. Fig. 5. Sternal process between posterior gonopods of *B. laminata.*

Chamberlin collection (now at U.S. National Museum?), examined. There is no John Day Creek in Douglas Co., but there is a town named Days Creek, and a stream of that name, a tributary of the South Umpqua River. Probably this is the type locality, and not the John Day River of Oregon's semiarid northeast.

Description: Male from 10 mi east, 6 mi north of Gold Hill, Jackson Co., Oregon: Length, 7.0 mm. Ocelli 14 on each side (a series of males from several localities had ocelli numbers from 14-17). Legpair 3 much enlarged, femora swollen and bowed mesad, without obvious processes. Legpair 4 enlarged, but smaller than legpair 3, femora not strongly curved, bearing small fungiform basal knobs mesally. Legpairs 5-7 only slightly larger than postgonopodal legs, without processes. Anterior gonopods simple, subtriangular, acuminate, curved posteriolaterad (Fig. 1). Posterior gonopod colpocoxites appearing 3-branched (Fig. 2), flagellar branch (*f*) long, prominent; sheathing structure (*s*) reduced, completely separated from anterior process (*c*), which is simple and without branches. Posterior gonopod sternum with a large T-shaped process (*T*). Pigmentation typical.

Females similar to males, slightly larger and more robust.

Distribution: (all collections by E. M. Benedict) OREGON: *Josephine Co.,* 0.3 mi S, 2.5 mi E O'Brien, T40S/R8W/Sec 28, elev. 1400′, 18 December 1971, ♂♂ ♀♀. *Coos Co.,* 3 mi N, 2 mi W North Bend, T24S/R13W/Sec 27, sea level, 15 January 1972, ♂. *Douglas Co.,* Island Campground, 0.5 mi S, 1.0 mi E Steamboat on Ore. Rt. 138, T26S/R1E/Sec 5, elev. 1200′, Berlese of maple, dogwood dubb, 20 October 1971, ♂♂; Boulder Flat Campground, 3 mi E, 10 mi S Steamboat, T26S/R2E/Sec 13, elev. 1700′, Berlese red alder, vine maple duff, 30 October 1971, ♂; 4 mi S, 9 mi E Steamboat on Ore. Rt. 138, T26S/R2E/Sec 23, elev. 1600′, Berlese conifer and oak duff, 30 October 1970, ♂♂ ♀♀. *Jackson Co.,* 10 mi NW Central Point on Ore. Rt. 234, T35S/R2W, elev. 1200′, 22 January 1973, ♂♂ ♀. Lewis Buckley Farm, 1 mi S Ruch on Ore. Rt. 238, T38S/R3W, elev. 1700′, Berlese litter, duff, soil, 13 November 1971, ♂; Upper Applegate Grange, 6 mi S Ruch, T39S/R3W/Sec 15, elev. 1600′, Berlese mixed litter, 13 November 1971, ♂♂ ♀♀; Buckley County Park Rest Area, 3.5 mi S Ruch on Upper Applegate Rd., 2 mi off Ore. Rt. 238, T39S/R3W/Sec 15, elev. 1600′, Berlese white alder, willow duff, 13 November 1971, ♂♂; French Gulch, For. Ser. Rd. 420, 3 mi N Copper, T40S/R4W/Sec 36, elev. 1900′, Berlese Oregon oak duff, 13 November 1971,

♂ ♀; 15 mi SW Ruch on Upper Applegate Rd., T40S/R3W/Sec. 8, elev. 1800′, Berlese duff, debris, moss, bark, 13 November 1971, ♂ ♂; 10 mi E, 6 mi N Gold Hill on Ore. Rt. 234, T35S/R1W/Sec 17, elev. 1300′, 22 January 1972, ♂ ♂ ♀♀; 6 mi E, 3 mi N Gold Hill, T35S/R2W/Sec 27, elev. 1200′, 22 January 1972, ♂ ♂.

Notes: Chamberlin's brief discussion of the leg modifications is confusing. In the generic diagnosis leg 5 is described as being "normal" while in the specific diagnosis, leg 5 is described as "less thickened, (the) fourth joint with a . . . subconical process on mesal side toward proximal end . . ." Thus *B. oregona* is immediately excluded from the very genus it is being described under! Chamberlin saw 14 ocelli on each side, and gave the size as 7-7.5 mm. The male holotype is in poor condition.

Where ecological data is available, the species appears to occur in duff from deciduous trees. Many samples of coniferous duff did not yield *Bollmanella oregona.* The species has been collected at elevations from sea level to 1900′, and thus appears to be primarily a coastal or river valley species, since many samples from higher elevations did not contain *B. oregona.* This is the most widespread and common species of *Bollmanella.*

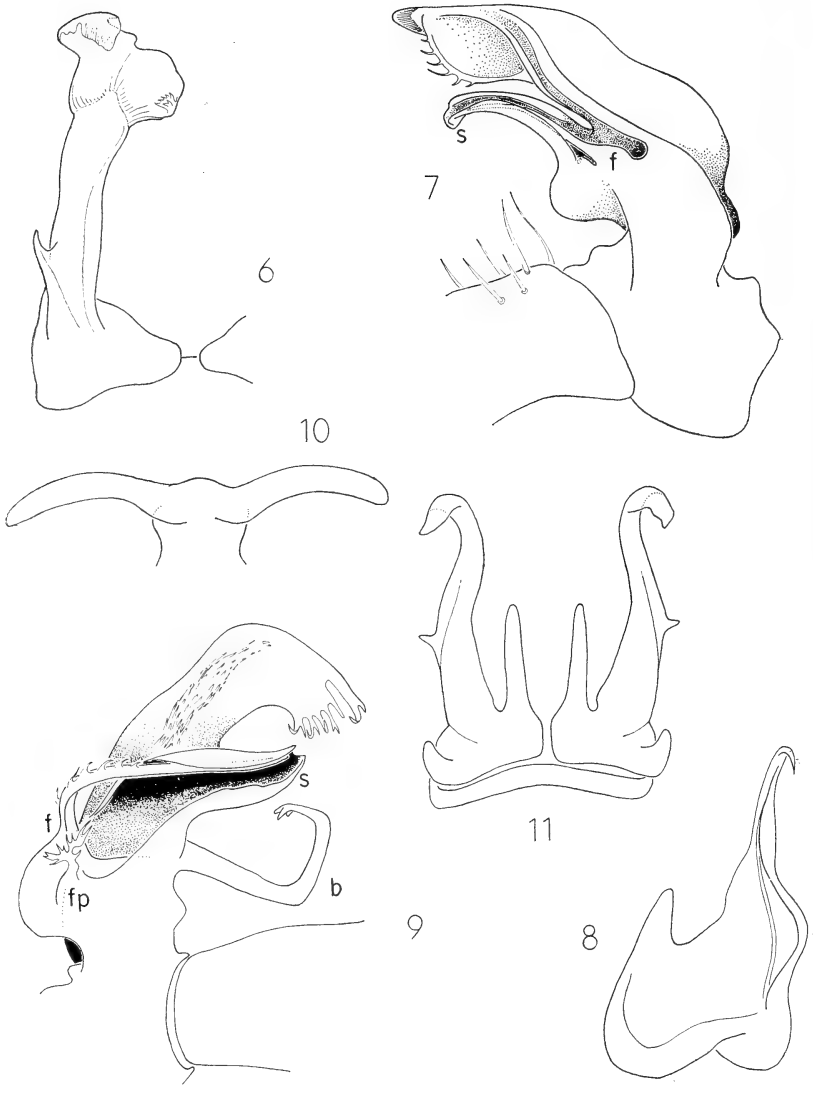
Bollmanella reducta n. sp.

Figs. 3, 4

Type: Male holotype from 2 mi north, 6 mi east of Ashland, Jackson Co., Oregon (T38S/R3E/Sec 27), collected at an elevation of 1200′ by E. M. Benedict, 27 December 1971.

Description: Male holotype. Length, 5.0 mm. Ocelli 8 on each side of head. Legpair 3 much as described for *B. oregona.* Legpair 4 less enlarged, lacking basal femoral knobs present in *B. oregona.* Legpairs 5-7 of normal size. Anterior gonopods (Fig. 3) much as in *oregona,* but gonopod tip blunter. Posterior gonopod colpocoxites (Fig. 4) of reduced complexity when compared to following species; flagellum (*f*) short; sheathing structure (*s*) fused anteriorly to body of colopocoxite, which is broad and laminate, with minute teeth distally. T-shaped process of sternum present, but broken in making temporary slide of gonopods. Pigmentation light.

Distribution: Known only from the type locality. The holotype came from a Berlese sample of Oregon oak and buckbrush litter on a steep slope.



Figs. 6, 7. *Bollmanella laminata.* Fig. 6. Right anterior gonopod, posterior view. Fig. 7. Right posterior gonopod, posterior view. Figs. 8-10. *B. unca.* Fig. 8. Left anterior gonopod, posterior view. Fig. 9. Left posterior gonopod, posterior view. Fig. 10. Sternal process between posterior gonopods. Fig. 11. Anterior gonopods of *B. bifurcata,* posterior view.

Bollmanella laminata n. sp.

Figs. 5-7

Types: Male holotype, female paratype and other specimens from 0.3 mi west of Southern Pacific overpass on Rt. 26, 3 mi east of Timber, Washington Co., Oregon (T3N/R5W/Sec ?) collected at an elevation of 900′ by E. M. Benedict, 27 November 1971.

Description: Male holotype. Length, 6.5 mm. 17 ocelli on each side (a second male had 20 ocelli on each side). Legpair 3 much swollen, femora enlarged and arched mesad, with sharp mesoposterior tooth near each apical end. Legpair 4 normal in size, without processes. Legpairs 5-7 of normal size and form. Anterior gonopods (Fig. 6) erect, bearing lateral tooth near base; apex expanded into thin lamina recurved and folded on lateral edge. Posterior gonopod colpocoxites (Fig. 7) showing relationshhip to the previous two species, flagellum (*f*) short, sheath (*s*) completely separate from anterior body of colpocoxite, as in *B. oregona.* T-shaped process of sternum with arms sharply curved ventrad (Fig. 5). Pigmentation light, much lighter than *B. oregona* but darker than in *B. reducta.*

Female similar to male in nonsexual characters, somewhat more robust and larger.

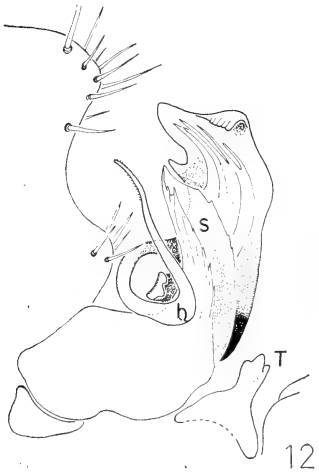
Distribution: Known only from the type locality. The types came from a sample of vine maple and Douglas fir duff.

Bollmanella unca n. sp.

Figs. 8-10

Types: Male holotype, juvenile female, and a second male from 4.5 mi east of Wells Creek Ranger Station, Douglas Co., Oregon (T22S/R9W/Sec 15), elev. 300′ collected 11 December 1971 by E. M. Benedict.

Description: Male holotype. Length, 7.0 mm. 14 ocelli on each side of head (second male from type locality had 12 ocelli on each side). Legpair three greatly enlarged, femora strongly bowed mesad, more so than in *oregona,* base of each femur so swollen and curvature so extreme that appearance of large basal knob is presented. Legpair 4 much as in *oregona,* but femoral knob larger, more flattened. Legpairs 5-7 of nearly normal size, lacking knobs. Anterior gonopods (Fig. 8) broadly triangular at base, tapering to curved, sharply aciculate apex, deeply excavated mesoposteriorly at base, with mesal angle drawn ventrad into short, blunt process. Posterior gonopod colpocoxites (Fig. 9) complex; flagellum (*f*) large, long, with mem-



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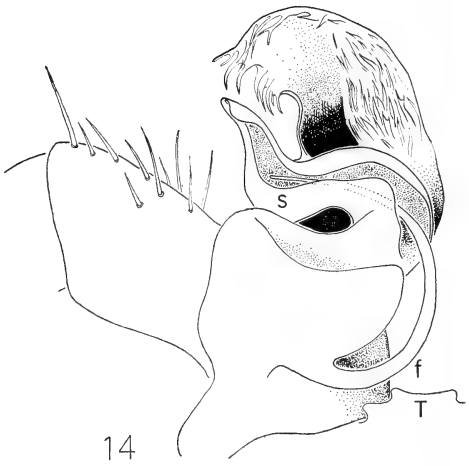

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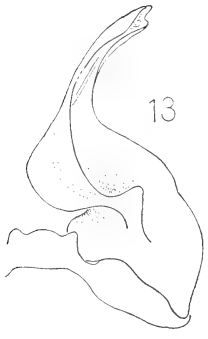

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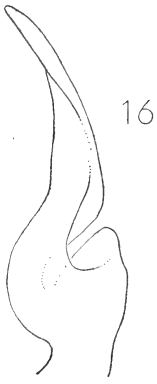

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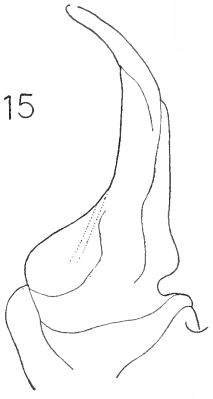

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Fig. 12. Right posterior gonopod of *Bollmanella bifurcata,* posterior view. Figs. 13, 14. *B. bella.* Fig. 13. Left anterior gonopod, posterior view. Fig. 14. Right posterior gonopod, posterior view. Figs. 15, 16. *B. camassia.* Fig. 15. Right anterior gonopod, posterior view. Fig. 16. The same, lateral view.

branous serrations on mesal edge; irregular chitinized membrane at base (*fp*); sheath (*s*) large, enfolding flagellum, basally fused to anterior part of colpocoxite. Near point of fusion is large basal process (*b*) which is sharply elbowed and distally trifucate; colpocoxite with fimbriate ridge mesally and irregular, apical, laminate teeth. T-shaped process from posterior gonopod sternum much the largest in genus, arms extending laterad (Fig. 10). Pigmentation typical, but somewhat darker than in *B. oregona.*

Mature females not collected.

Distribution: In addition to the type locality: OREGON: *Douglas Co.,* Mack Brown County Park on Umpqua R., T25S/R7W, elev. 400′, 7 February 1972, E. M. Benedict, ♂.

Notes: Collections at both sites were from Oregon oak duff.

Bollmanella bifurcata n. sp.

Figs. 11, 12

Types: Male holotype, female paratype and other specimens from 2 mi west of Joseph along Hurricane Creek, Wallowa Co., Oregon, collected 23 November 1968 by D. R. Malcolm.

Description: Holotype male. Length, 9.2 mm. 20 ocelli on left side of head, 21 on right side. Legpairs 3 and 4 enlarged, approximately same size, both with small mesal femoral knobs. Legpairs 5-7 decreasing in size, legpair 7 normal in size and form. Anterior gonopods (Fig. 11) upright, curved, with small lateral spine and large blunt mesal branch, presenting bifurcate appearance with telopodite. Posterior gonopod colpocoxites (Fig. 12) rather smaller than usual, flagellum not observed, probably concealed by large sheath (*s*) which is free from coxite for most of its length. Body of coxite with large, spirally curved basal branch (*b*) bearing near its base a curved lamina. Sternal process (*T*) much less prominent than in other species. Pigmentation very light.

Females as usual, similar in general appearance to males, but slightly larger and more robust.

Distribution: Known only from the type locality.

Note: This species is far removed from the other members of the genus, being found in the foothills of the Wallowa Mountains in extreme northeastern Oregon. This part of the state has not been much explored by biologists, and other species of *Bollmanella* may well ocur in other isolated mountain ranges. The region is also close to that studied by Loomis and Schmitt (1971), and in which they

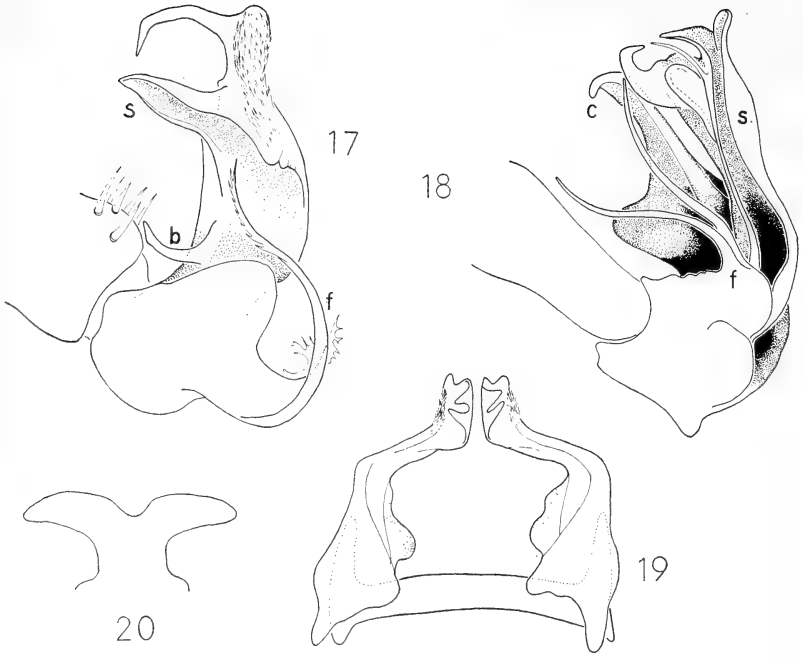

Fig. 17. Right posterior gonopod of *Bollmanella comassia,* posterior view. Figs. 18-20. *B. complicata.* Fig. 18. Right posterior gonopod, posterior view. Fig. 19. Anterior gonopods, posterior view. Fig. 20. Sternal process between posterior gonopods.

found several highly unusual chordeumid species. *Bollmanella bifurcata* shows some intermediacy in size, pregonopodal leg modifications, and gonopod form between species of *Bollmanella* and *Taiyutyla,* and this may suggest that the two genera could be difficult to keep separate in eastern Oregon. Loomis and Schmitt (1971) described *Taiyutyla curvata,* from Montana, but it does not appear (from their illustrations) to be very much like *B. bifurcata.*

The types and several other specimens of both sexes were taken from cottonwood litter, in a riparian situation.

Bollmanella bella n. sp.
Figs. 13, 14

Types: Male holotype and a juvenile female (not designated as a

paratype) from 11 mi east and 4 mi west of Allegany, Company Road 5000 on the Weyerhauser Millicoma Tree Farm (T24S/R9W/Sec 18), at the Douglas and Coos Cos. boundary, Oregon, 20 November 1971, by E. M. Benedict.

Description: Male holotype. Length, 6.0 mm. Ocelli 17 on both sides of head. Femora of legpair three very much enlarged and bearing small knobs mesally just above inflection point of curve. Legpair 4 somewhat smaller, femora with large capitate knobs just distad of midpoint on mesal side. Legpairs 5-7 only slightly larger than normal. Anterior gonopods (Fig. 13) much as usual, curved laterad, acuminate. Posterior gonopod colpocoxites (Fig. 14) somewhat larger than in other species, flagellum (*f*), long, curved into sigmoid sheath (*s*); body of coxite with mesal fimbriate ridge, apically laciniate. Sternal process (*T*) small. Pigmentation dark.

Mature females definitely belonging to this species were not collected.

Distribution: In addition to the type locality, a single female from 6 mi east of Allegany on the Millicoma Tree Farm may also be this species.

Notes: The type was taken in a Berlese sample of myrtle and *Rhododendron* litter and duff; the second female referred to above also came from myrtle litter.

Bollmanella camassia n. sp.

Figs. 15-17

Types: Male holotype and female paratype from 2 mi northeast of Camas Valley on Oregon Rt. 42 (T29S/R8W), collected at an elevation of 1400′ by E. M. Benedict, 19 February 1972.

Description: Male holotype. Length, 7.0 mm. Ocelli 12 on both sides of head. Legpair 3 much less enlarged than in other species, with a small knob near distal ends of femora, which are evenly curved and swollen. Legpair 4 only slightly larger than normal, femoral knobs basal in position. Legpairs 5-7 normal in size and form. Anterior gonopods (Figs. 15, 16) simple, acuminate, curved; in lateral view, gland channel (?) originates in deep anteriolateral depression. Posterior gonopod colpocoxites (Fig. 17) with long flagellum (*f*) bearing irregular membranous process near base; sheath (*s*) arising from midpoint of coxite; coxite bears a strong decurved process apically and a small basal branch (*b*). Sternal process not observed, perhaps absent. Pigmentation as in *B. oregona.*

Female as usual, somewhat larger and more robust than male.

Distribution: Known only from the type locality.

Notes: The holotype came from a Berlese sample of vine maple, willow, and Madrone duff near a grove of Douglas firs.

Bollmanella complicata n. sp.
Figs. 18-20

Types: Male holotype and paratype from 1 mi west of Bayshore, 4 mi north of Shelton, Mason Co., Washington, collected 25 November 1967, by E. M. Benedict.

Description: Male holotype. Length, 6.0 mm. 13 ocelli on each side of head. Legpair 3 enlarged as usual, but less curved mesad. Legpair 4 nearly normal in size and form, without femoral knobs. Legpairs 5 and 7 of normal size and form. Anterior gonopods (Fig. 19) sharply elbowed mesad after crossing (*in situ*) laterad of posterior gonopod colpocoxites; apically laminate. Posterior gonopod colpocoxites (Fig. 18) most complex in genus; flagellum (*f*) with two branches about equal in size, one of these may be the homolog of the basal lamina seen in other species; sheath (*s*) free, apically with complex series of hooked, bulbous and aciculate processes; body of coxite (*c*) very broad basally, flared, tapering to hooked apex. Sternal process (Fig. 20) large, arms searly horizontal. Pigmentation light.

Females not collected.

Distribution: Known only from the type locality.

Notes: The holotype and paratype were collected from a Berlese sample of oak and pine duff.

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A NEW GENUS OF PRIMITIVE MELOIDAE FROM WEST TEXAS (COLEOPTERA)[1]

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The beetle described here is the most unusual meloid I have ever encountered. When Henry Howden sent me a male, several years ago, I examined it and placed it among the unidentified pedilids. But re-examination in relation to the pedilids convinces me that it is indeed a meloid, and probably one of considerable evolutionary interest. Since I first saw a specimen, Richard Selander (1966) has published a comprehensive study of the meloid subfamily Eleticinae, which is generally unfamiliar to students of North American beetles. The Eleticinae have some characteristics that are different from those of conventional meloids; part of these are shared by the new genus described here. The Eleticinae are so different from other Meloidae that Selander suggests that relationship would best be indicated if they were set up as a separate family, or as a subfamily of weight equal to one combining all other meloids. But, in the interest of avoiding major changes before relationships are certain, he has (1964, 1966) followed a course of recognizing three subfamilies of Meloidae: Eleticinae, Meloinae, and Nemognathinae, with the Eleticinae considered the most primitive. The group has a disjunct distribution in the Old World (mainly Africa but including a few species in Southeast Asia) and South America, both of the tribes he recognizes in his 1966 paper having members on both sides of the Atlantic. This relict type of distribution certainly supports his opinion that this is an ancient group. Unfortunately, there are no observations on the behavior of the subfamily, and the larval associations that have been made are based on supposition rather than observation. So only adult structures can be used in classification.

Perhaps the single thing that is most meloid-like about the insect described here is the shape and conformation of the head (Fig. 2, 3). The only thing that is unusual at all is that the eyes are more coarsely faceted than is usual for the family. The general body shape (Fig. 1) is also not greatly different from that of some other meloids; the main points of difference are those of the Eleticinae: cuticle much firmer

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than usual and elytra conjointly rather than separately rounded. To these features must be added a uniform brown coloration, unusually small size, less than 5 mm, quite dense and deep punctures over the whole dorsal surface, and moderately dense, fine pubescence, all unusual for the family but found in some Eleticinae.

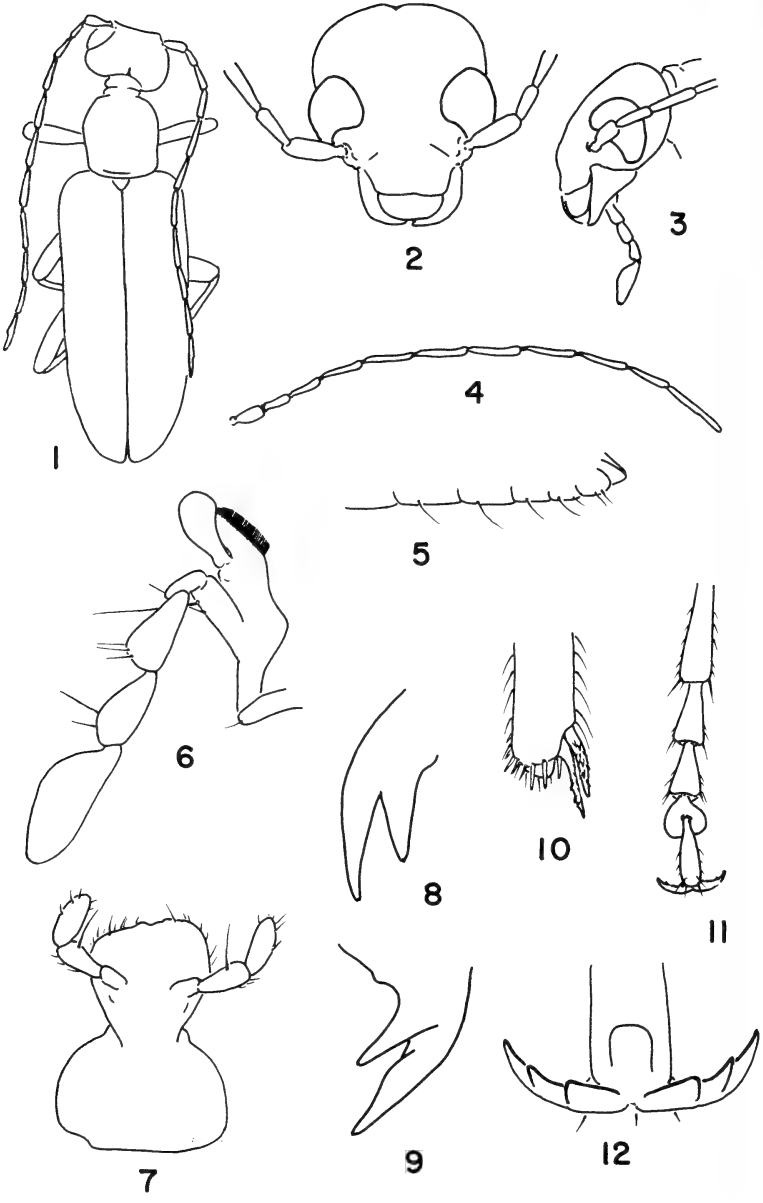
The combination of these features and lack of a separate blade on the tarsal claws would make identification of the genus as a meloid almost impossible with existing keys to the family, even if one had a good representation of other genera for comparison. In fact, I have tried repeatedly to find reasons for excluding it from the family, but have then been faced with the decision that it is more like meloids than it is like any other family known to me. So I am describing it as a meloid, possibly assignable to the subfamily Eleticinae, but not definitely assignable to this subfamily nor to either of the included tribes recognized by Selander (1966). It is my hope that the existence of a population in a relatively accessible location will ensure that both bionomics and behavior will come under study and that these will permit more exact assignment.

Since it is almost inevitable that comparison will be made with the Eleticinae and that Selander's 1966 paper will provide the basis for comparison, I have attempted to follow Selander's terminology and his pattern of description. However, I have not attempted to review the whole subfamily, and therefore may have strained too far to see structures that are obvious in the subfamily and not necessarily in this genus. The bases for measurement also follow Selander's paper.

Genus **Thambospasta,** new genus

Characteristics. Small, less than 5 mm, slender beetles (Fig. 1) of the family Meloidae and doubtfully of the subfamily Eleticinae as defined by Selander (1966); monochromatic brown; head, pronotum, and elytra densely, moderately deeply and moderately finely punctate; with simple slightly curved decumbent setation, also monochromatic. Mentum, palpi, coxae, trochanters, and abdominal sterna (Fig. 5) with single to double, long erect tactile setae, those on mentum and abdomen sublateral. Head just perceptibly longer than broad (Fig. 2); vertex not inflated, its base subtruncate. Eyes moderately large, length 1 1/3 frontal ocular distance in male, 1 1/10 in female; anterior margin slightly excavated (Fig. 3); facets coarse and separate, ca. 8 across narrowest portion. Antennae slender, filiform; segment X 1/5 as wide as long (Fig. 4) in male; less slender

in female, segment X 1/2 as wide as long. Clypeus separated from frons by a depression only, with a narrow, thin, shiny shelf over base of labrum; labrum flat, not emarginate at apex. Mandibles half as long as head from top of vertex to anterior mandibular articulation; shallowly indented on mesal margin just basad of middle; prostheca moderately long, reaching beyond middle of mesal margin; molar lobe small but distinct; mesal margin without teeth but apex bluntly double-pointed, chisel-like, the mesal face flat for a small zone before apex; lateral margin almost evenly curved from base, with moderately dense setae. Maxillary palpi (Fig. 6) four-segmented, basal segment small, second and third subequal, last long, narrowly securiform. Galea simple, of but one segment. Labium (Fig. 7) with ligula apparently entire, blunt; mentum not strongly produced laterad. Pronotum 1/5 longer than wide, ca. 9/10 as wide as vertex, feebly subhexagonal in outline; disk feebly convex except for impressed midline. Front coxal cavities open externally, closed internally. Mesosternum obtusely angulate at anterior apex. Mesepisterna in contact medianly; anterior marginal area with a complete curved ridge from dorsal edge to near midline, subparallel to main ridge but converging toward it near midline. Apex of elytra simple in both sexes. Hind wings (Fig. 13) fully developed in both sexes; apical region 1/3 wing length; stem of media (M) short but distinct; crossvein r present and radial cell closed; base of $2A_2$ strongly developed, forming a closed cell ($1A_3$) with a crossvein from 1A; $3A_1$ not combined with $2A_3$, apparently present as a short branch which with a crossvein from $2A_3$ forms a closed cell . Male fore tibiae with two unmodified spurs (Fig. 10). Hind tibial spurs slender, essentially equal. All spurs with fine microspines (Fig. 10). Tarsal formula 5-5-4. Penultimate tarsal segment (Fig. 11) forming a flat, truncate lobe, the last segment arising from near middle of its dorsal surface. All tarsal claws with a very blunt basal tooth; those of fore and middle tarsi with a longer pointed tooth in addition (Figs. 8, 9, 12). There is no vestige of a ventrolateral lobe or blade. Abdominal sternum III excavated for hind coxae, the excavation bordered by a fine ridge. Male abdominal tergum VII weakly sclerotized, its apex slightly curved, at least this tergum with a micropubsecent area that is not divided on midline. All terga before VII weakly sclerotized; at least part seem to have the same kind of micropubescence. Male sternum VII truncate across apex, simple on disk; tergum VIII evenly sclerotized from very near base, bluntly ogival; sternum VIII sharply angular posterolaterally, its disk simple and its apex just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perceptibly emarginate between the angulations; tergum IX small, undivided and weakly sclerotized; sternum IX Y-shaped with broad lateral arms. Male genitalia (Fig. 14) with gonostyli fused dorsally from base to beyond middle; base of fused gonostyli produced posteriad on dorsal side in a process that surpasses the gonostyli and bears three dorsal and ca. 9 lateral short, stout setae on each side; gonocoxal plate cupped, ca. 1/2 as long as gonostyli. Aedeagus (Fig. 15) long, symmetrical, downcurved toward base, movable in relation to gonostyli; with two oblique lateral ridges on each side toward apex; secondary gonopore apparently apicodorsal; there is no indication of a sclerotized rod or projection from the internal sac in this region; dorsal surface of aedeagus apparently open for most of its length. Female abdominal segment VIII retracted into apex of abdomen, weakly sclerotized, its sternum with a long, slender apodeme (Fig. 17); ovipositor (Fig. 16) well-developed, long, with one-segmented gonostyli.

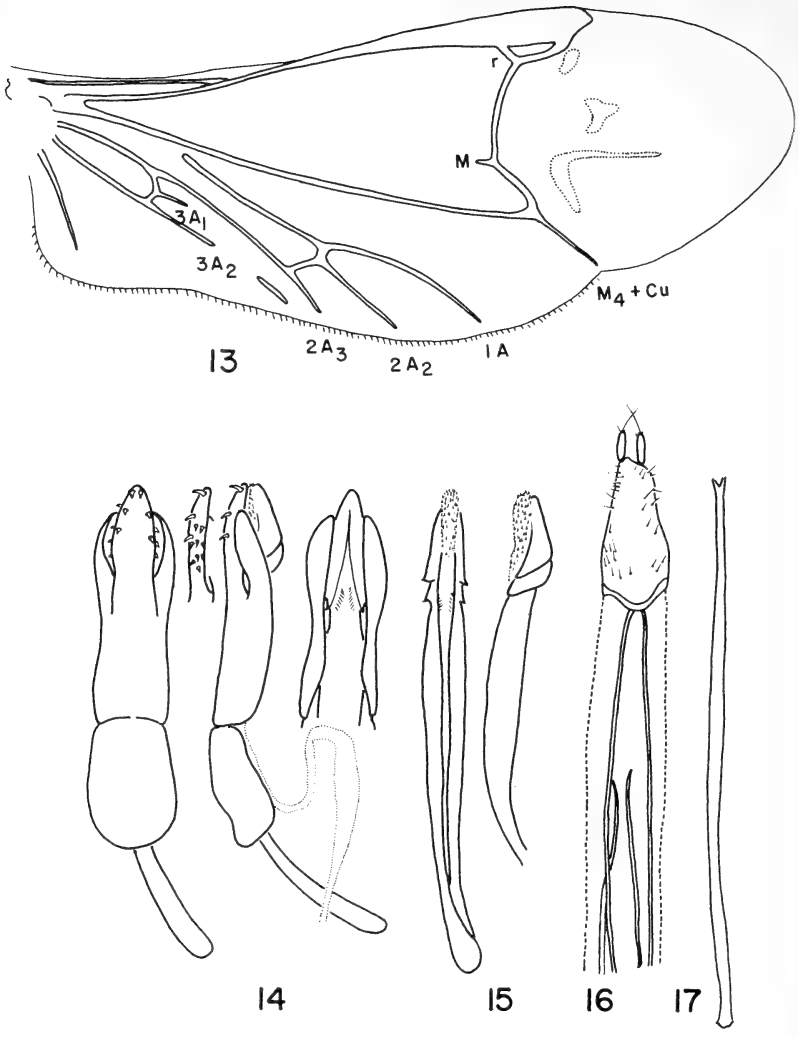
Type species. *Thambospasta howdeni* new species; fixed by present designation.

Remarks. This genus contains only the type species, described below. It is known from both sexes.

Thambospasta howdeni, new species

Male. Entirely rufescent brown except for black eyes, only tips of mandibles appreciably darker; pubescence concolorous, fine, and therefore inconspicuous. Length 3.6-4.4 mm, mean 3.88, SD 0.29, holotype 4.4. Surface generally shiny, but deep punctures dull it somewhat. Punctures on head uniform, flat-bottomed, ca. 0.04 mm across, 0.05 center to center, even across midline; midline indicated only as a notch on vertex. Antennal calluses distinct, grading into a small elevation over base of antenna, with punctures like rest of head. Head depressed across front between antennae, in region of frontoclypeal suture, which is not visible, punctures extending evenly across whole region; clypeus ending in a smooth shelf ca. 0.04 mm wide and flat, over base of labrum. Eye facets almost exactly 0.03 mm in diameter, very regularly arranged. Punctures of pronotum just

Figs. 1-12. *Thambospasta howdeni.* 1, dorsal view of holotype male; 2, head of holotype in front view; 3, same in oblique lateral view; 4, antenna of paratype male; 5, profile of abdominal sterna of holotype; 6, maxilla of paratype male; 7, labium of same; 8-9, pieces of tarsal claws of same; 10, tip of front tibia of same; 11, front tarsus of same; 12, detail of front tarsal claws, ventral view.



Figs. 13-17. *Thambospasta howdeni.* 13, hind wings of paratype male; 14, genitalia of paratype male in dorsal, lateral, and ventral views, with inset of details of median process; 15, aedeagus of same in dorsal and left lateral views; 16, ovipositor of allotype female; 17, anterior apodeme of abdominal sternum VIII of same; Figs. 14-17 at 60× magnification.

perceptibly smaller, 0.03-0.04 mm across and not as distinctly flat-bottomed. Punctures of elytra deep across base, shallower behind, ca. 0.03 mm across and 0.05 center to center, round-bottomed, closer to 0.04 mm across near base, evenly distributed. Pubescence of upper surface slightly curved, decumbent, ca. 0.07 mm long, fairly inconspicuous because it is not at all flattened and is concolorous with cuticle. Antennae with moderately dense suberect setae ca. 0.05 mm long from segment 2 to apex, a few such setae on first. Punctures of underside of thorax more rugulose, fairly shallow, ca. 0.02-0.03 mm across; those on abdomen smaller and finer, mose distinct from each other, ca. 0.02 mm across and 0.03 center to center.

Female. Known only from allotype, 4.6 mm long. Antennae generally shorter and less slender, without the suberect setae of the male. Unfortunately, most of antennae lost after description. Measurements in 0.01 mm, base to apex: 55/20, 34/16, 44/15, 50/15, 49/15, 46/15, 47/15, 42/15, 39/15, 32/15, 54/15. Last segment with little indication of the change of thickness seen in the male. Eyes distinctly smaller and noticeably narrower than in male. Maxillary palpi smaller, last segment 0.24 mm long, 0.29 in male holotype, which is slightly smaller.

Holotype male, allotype female and 11 male paratypes, Big Bend N[ational] P[ark], TEX[AS], 1850′, Boquillas, May 23, 1959, light; Howden & Becker; 3 male paratypes same but May 13. Holotype, allotype, and 11 paratypes in Canadian National Collection, 3 paratypes in collection of author.

Discussion. If this beetle is really a member of the family Meloidae, it is probably one of the most primitive yet discovered. Of the features that Selander (1966) lists as common to all meloids, including Eleticinae, *Thambospasta* conforms in only three: head with a well-developed vertex and narrow neck; pronotum not bordered laterally [with exceptions in Nemognathinae]; and female gonostyli one-segmented. It resembles Eleticinae but not the other subfamilies in that the cuticle is more heavily sclerotized; abdominal sternum III is excavated and margined to accommodate the hind coxae; the female has a distinct ovipositor; and in the following characteristics of the venation of the hind wings: vein $2A_2$ present and joined to 1A by a crossvein (also in Meloinae: Lyttini: Prolyttina); and $3A_1$ connected to base of 3A (in Eleticinae except Spasticini: Protomeloina and in some non-eleticines, apud Selander). It is very similar to Eleticinae: Spasticini: Anthicoxenina in that the male gonostyli are fused dorsally at the base and have a median dorsal projection; this

feature is unknown elsewhere in the family. It is more like Meloinae and Nemognathinae than Eleticinae in that the apices of the elytra are not swollen and provided with a pit in the male (as they are in all Eleticinae but Spasticini: Anthicoxenina: *Iselma*).

It would be difficult to associate *Thambospasta* with *Iselma* in the Eleticinae on the basis of the similarity of the male genitalia and lack of elytral pits, because *Thambospasta* males have abdominal tergum VIII heavily sclerotized and would therefore become associated with Eleticini, the other tribe in the subfamily in Selander's classification. It differs from all Eleticinae in that vein $2A_2$ of the hind wings is joined to the base of 2A, a condition approached in some Eleticinae, however, and in being nocturnal rather than diurnal, as the few Eleticinae for which records are available seem to be. If Selander's $2A_3$ of the Nemognathinae: Nemognathini: Zonitina: *Pseudozonitis* were counted as a primitive vein, rather than a specialization as he argues (1966), that genus would also have $2A_2$ joined to the base of 2A.

Returning to the features that Selander lists as being shared by all subfamilies of Meloidae, *Thambospasta* differs in several probably important ways: fore coxal cavities open externally but closed internally (open in all others); female abdominal sternum VIII with a long anterior apodeme (none at all in others); last segment of maxilliary palpi narrowly securiform (never securiform in others); and cross-vein r apparently present (never in others). It also is unlike most Meloidae in that the male genitalia lack a sclerotized ejaculatory rod (lacking also in Eleticinae: Eleticini: Eospastina: *Eospasta* and in many Nemognathinae); and in that the tarsal claws lack a process arising from the lateral side of the base (lacking also in some specialized Meloinae and Nemognathinae). A possible third feature is that the aedeagus lacks a hook on its ventral side at or near the apex, a condition that is universal in Meloinae and present also in part of the Eleticinae. A feature not mentioned by Selander that is probably universal in Meloidae is the lack of microspines on the tibial spurs such as are seen in *Thambospasta*.

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POLYMORPHISM IN *STELOPOLYBIA AREATA* (HYMENOPTERA, VESPIDAE)

By Robert L. Jeanne[1] and Robert Fagen[2]

Polymorphism in the social Hymenoptera has been defined as the occurrence within a single colony of two or more distinct morphological forms, or castes, belonging to the same sex (Wilson 1953). Wilson (1953) has pointed out that polymorphism arises out of the occurrence of allometry (differential rates of growth of two parts of the body) over a sufficient range of intranidal size variation to produce morphologically distinct forms at the extremes of this size range. The underlying size variation is due in most cases to differences in larval nutrition (Michener 1961; Wilson 1971). Polymorphism is the morphological adaptation to the functional division of tasks among the members of a colony (Wilson 1953). The most fundamental polymorphism is the separation of the reproductive caste (queens) from the non-reproductive caste (workers). This is followed, most notably in the ants, by the evolution of more or less distinct castes among the workers.

Among the wasps polymorphism appears to be limited to the queen-worker dimorphism, where it is most pronounced in the Vespinae (Wilson 1971). Among many of the Polistinae there is no detectable difference, either in size or in morphology, between functional queens and workers (Richards and Richards 1951). The present paper reports the occurrence of complete queen-worker dimorphism in colonies of the polistine species *Stelopolybia areata* (Say) from Mexico.

Materials and Methods

Stelopolybia areata ranges from Mexico south to northern South America (Ducke 1910). The four colonies available for the present study were collected near San Andres Tuxtla in southern Veracruz, Mexico, in January and February 1973. During these months the nests are occupied by adult females only. No brood or males are present. Population size and composition for each colony are given

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Table I. Size and Composition of Adult Populations of *Stelopolybia areata* colonies.

Colony No.	Date Collected	No. Adults Collected	No. Queens Collected	Percent Queens	Estimated Total Adult Population
707	2 Feb. 1973	5884	716	12.2	7000
710	15 Jan. 1973	7950	515	6.1	8500
725	23 Feb. 1973	4711	257	5.5	6000
731	21 Feb. 1973	4227	503	11.8	6000

in Table I. A description of the nest of this species and notes on colony cycle are published elsewhere (Jeanne 1973).

In a mass of anaesthetized adults, queens can readily be picked out by virtue of their larger size and distinctive morphology and coloration. Random dissections of queens and workers always showed that the former had well-developed ovaries and full spermathecae, while the latter had undeveloped ovaries and empty spermathecae.

For the present study random samples of queens and workers from each colony were measured and compared. Length of alitrunk was chosen as a measure of body size. This was measured from the front of the humeral collar to the furthest posterior extension of the propodeal valves, as seen from the side. This dimension was preferred as a measure of body size for several reasons. First, the alitrunk is the longest rigid structure of the body, hence is not subject to error due to varying degrees of distension of the gut, or to differences in body position. Second, it is not likely to be an allometric growth center, unlike in the ants, since both queens and workers are winged. Any functional difference in use of wings by workers and queens is less likely to be reflected by allometric differences in size of the thorax than in differences in the wings themselves. Finally, it is preferred to wing length, used in other studies, because wings are subject to fraying at the tips in older workers, making them impossible to measure, and thus biasing the sample against older workers.

The most conspicuous morphologic difference between the two castes is the more bulbous first abdominal tergite (petiole) in the queens (Fig. 1). This is best reflected in its width at the widest point, as seen from above; hence this dimension was used as a measure of allometric growth.

All measurements were made on specimens pinned while fresh using an ocular micrometer at a magnification of 25×.

Fig. 1. *Stelopolybia areata* queen (left) and worker (right).

Standard methods and tests (Hays 1963) were used for computation and assessment of significance of regression slopes. Lewis (1960) presents techniques for the analysis of intersample differences between regression slopes; we used the following statistic to test the significance of intercaste regression slope differences.

Let $\hat{k}_{(i)}$ = estimated regression slope for i^{th} caste.

$\hat{\sigma}^2_{(i)}$ = sample variance in i^{th} caste of ln (tergite width) given ln (alitrunk length).

$\hat{\sigma}_{1(i)}$ = sample standard deviation of ln (alitrunk length) in i^{th} caste.

n_i = number of individuals of i^{th} caste sampled.

i = 1 for workers and 2 for queens.

Under standard assumptions of regression analysis (normality, homeoscedasticity, interindividual independence of measurements) the statistic

$$\frac{k_{(1)}\hat{\sigma}_{1(1)}\sqrt{n_1} - \hat{k}_{(2)}\hat{\sigma}_{1(2)}\sqrt{n_2}}{\sqrt{2}\sqrt{\frac{n\,\hat{\sigma}_{(1)} + n_2\hat{\sigma}^2_{(2)}}{n_1 + n_2 - 4}}}$$

has a t-distribution with $n_1 + n_2 - 4$ degrees of freedom.

Results

Coloration. Both castes are yellow with brown or black dark markings (Fig. 1). The yellow of workers, however, is a bright lemon yellow, while that of queens contains much more brown. The dark markings of workers are mostly black, while in queens they are dark brown, especially on the gaster. Thus, the dark and light coloration of workers is much more contrasting than that of queens.

On average the dark markings are slightly more extensive on the head and thorax of workers than of queens. On the other hand, the dark bands on the gaster are proportionately wider in queens than in workers. The dark band of the second abdominal tergite in workers has a pointed median posterior extension that is lacking in queens.

Body size. Results of the two measurements made are summarized in Table II. There is no overlap in size (length of alitrunk) of queens and workers in any of the colonies; thus the two castes are

Table II. Queen/Worker Dimorphism in *Stelopolybia areata.*

A. Length of Alitrunk

Colony No.	Queens N	Queens Average	Queens Range	Workers N	Workers Average	Workers Range	Queens/ Workers
707	45	4.22	4.02–4.37	45	3.63	3.29–3.75	1.16
710	49	4.10	3.83–4.29	60	3.57	3.29–3.75	1.15
725	23	4.13	4.02–4.29	50	3.68	3.41–3.83	1.12
731	50	4.19	3.98–4.33	50	3.68	3.33–3.83	1.14

B. Width of First Abdominal Tergite

Colony No.	Queens N	Queens Average	Queens Range	Workers N	Workers Average	Workers Range	Queens/ Workers
707	45	1.60	1.34–1.72	45	0.94	0.88–1.00	1.70
710	49	1.52	1.30–1.68	60	0.95	0.84–1.00	1.60
725	23	1.49	1.42–1.57	50	0.95	0.88–1.00	1.57
731	50	1.58	1.42–1.76	50	0.93	0.88–1.00	1.69

completely dimorphic with respect to this character. This is shown graphically in Fig. 2, where size-frequency distribution data for three of the colonies are grouped. (Colony 710, whose queens and workers are smaller than average, is omitted from Fig. 2 because its smallest queens overlap in size with the largest workers of two of the other colonies, obscuring the bimodality that exists within colonies.) The ratio of average length of alitrunk in queens to that in workers ranges from 1.12 to 1.16 for each of the four colonies sampled, with an overall average of 1.15.

Allometry. The width of the first abdominal tergite is proportionately much greater in queens than in workers. This is evident in the large queen/worker ratios with respect to this dimension (Table II). The regression of the width of the first abdominal tergite on alitrunk length has been computed for queens and workers of each of the four colonies, and the equilibrium constants (k, or slope of the regression line) are presented in Table III.

In all colonies the allometry of the worker caste is negative. For queens this shifts to strongly positive in all colonies except 725 (where small sample size may have biased the result). The intranidal differences in k for queens and workers are significant at the 1% level

Table III. Allometric Growth in *Stelopolybia areata*.

Colony No.	Regression slope (k) Queens	Workers	t	d.f.	Significance of Difference	Variance of x given y Queens	Workers	F	d.f.
707	1.51	0.70	−1.78	86	$0.05 < P < 0.1$	.001249	.000739	1.62	43,43
710	1.28	0.22	−3.28	105	$P < 0.002$	.001241	.001045	1.21	47,58
725	0.93	0.74	1.90	69	$0.05 < P < 0.1$	.000570	.001150	2.04	21,48
731	1.46	0.39	−3.16	96	$P < 0.002$	.001222	.000830	1.45	48,48

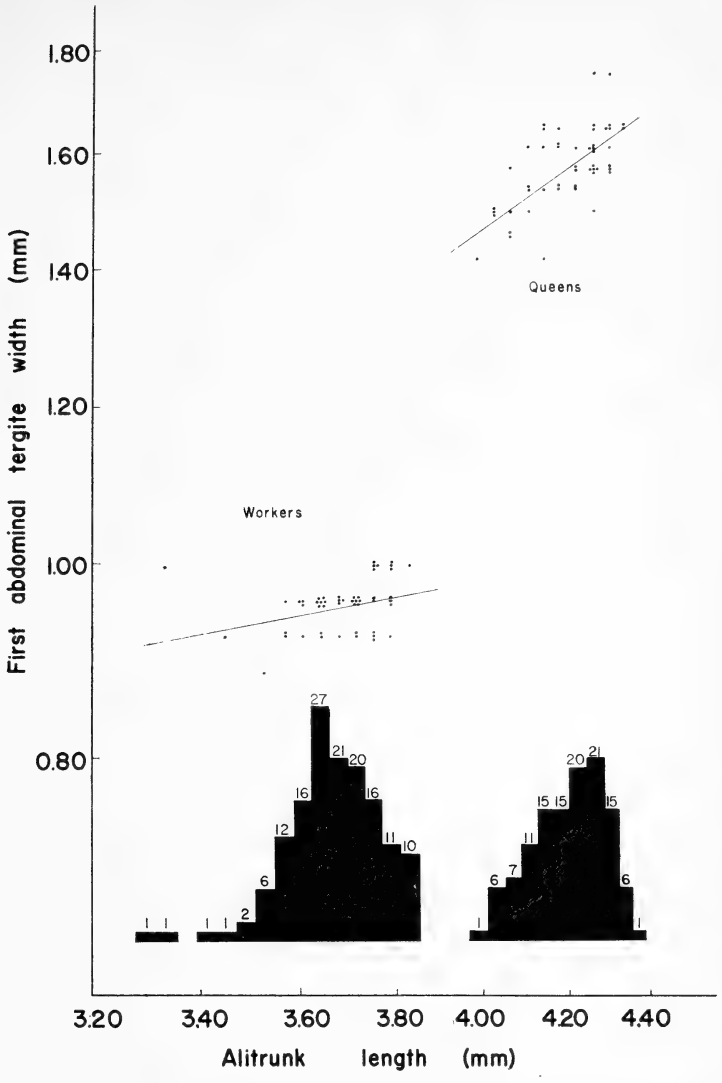

Fig. 2. Intranidal allometry and complete dimorphism in *Stelopolybia areata*. Log-log plot of first abdominal tergite width against alitrunk length for members of colony 731. Computed regression lines are shown. Bar graph gives frequency distribution of alitrunk length among queens and workers of three colonies (707, 725, 731). Numbers at the top of each bar give number of individuals.

for two colonies, and not quite significant at the 5% level for the other two (Table III).

A log-log plot of allometry in colony 731 is shown in Fig. 2. The lack of alignment of the computed linear regression lines suggests that the dimorphism in this species may have arisen out of triphasic allometry with a dropping out of intermediates (Wilson 1953).

Discussion

The positive allometric growth of the first abdominal tergite in queens probably has an adaptive significance for the reproductive role of this caste. The expanded width of this segment reflects a general increase in size of the gaster (Fig. 1), which is most easily explained as an adaptation to accommodate the well-developed ovaries. Blackith (1958) found a similar increase in body proportions toward the posterior of queens compared to workers for two species of *Vespula.*

The negative allometry of the first abdominal tergite in workers must have other causes, however. It is possible that the narrower, more petiole-like first segment in workers may permit a greater maneuverability of the gaster and hence the sting, a feature that could in turn be interpreted as an adaptation to the role of workers in defense. Presumably the evolutionary divergence of the two castes with respect to this character reflects an almost complete functional sparation of the reproductive and defensive roles.

The variance of the width of the first abdominal tergite given the length of the alitrunk is higher than that for ants (Wilson 1953). It resembles more closely the variance for certain halictine bees (Knerer & Atwood 1966). These differences may reflect a genetic component to the variability observed. In mononogynous ants all the workers of a colony are offspring of a single queen, and quite likely of a single male. In *S. areata,* however, since the colonies are polygynous, the individuals sampled do not all have the same parents, and thus represent a larger pool of genetic variability.

A comparison of the degree of polymorphism shown by *S. areata* with that of other vespids is of interest, though difficult because of the lack of comparability of measurements used from one study to the next. The Vespinae are biometrically the best known social wasps (e.g. Wright, Lee, and Pearson 1907; Thompson, Bell, and Pearson 1910, 1911; Blackith 1958). They also show the greatest degree of polymorphism. Blackith's results for *Vespula germanica* and *V. rufa* are probably typical (Blackith 1958). For the sake of comparison let

us choose his measurement of thorax width as a measure of body size. Confidence that this indeed is a good indication of body size is gained from the fact that the cube of the queen/worker ratio for this dimension closely approximates the ratio of the reduced body weights of the two castes. The ratio of queens to workers for this character is 1.37 and 1.34 for *V. germanica* and *V. rufa,* respectively, and compares with 1.15 queen/worker ratio for alitrunk length for *S. areata* (Table IV). Thus there is considerably greater separation of queens and workers with respect to average body size in *Vespula rufa* and *V. germanica* than in *S. areata.*

In the subfamily Polistinae the degree of polymorphism appears to range from virtually none to the degree of dimorphism shown by *S. areata.* Almost nothing has been done biometrically with the subfamily, with the exception of Richards and Richards' analysis of certain characters in some of the South American species (Richards and Richards 1951). The primary aim of Richards and Richards' analysis was to find reliable morphological characters that could be used to distinguish queens from workers. Queens were defined as having sperm in the spermatheca. In some species the two castes differed most significantly in the number of hamuli, while in others wing length, vertex width, mesonotum length, or shape of the first abdominal tergite were more reliable. Of the characters measured by Richards and Richards probably mesonotum length comes closest to being an indicator of body size. At any rate, it is most comparable to alitrunk length, used in the present study. If we use as an index of queen/worker dimorphism the ratio of average mesonotum length for queens to that for workers, the two species analyzed by Richards and Richards have values considerably below the ratio of queen to worker alitrunk length for *S. areata* (Table IV). Small but significant differences with regard to at least one character were found by Richards and Richards to exist between queens and workers in *Polybia bistriata, P. occidentalis occidentalis, Protopolybia pumila, P. minutissima, Brachygastra scutellaris,* and *Polistes canadensis* (Richards and Richards 1951).

Conclusion

Stelopolybia areata thus appears to have achieved a high degree of queen/worker dimorphism relative to other species of Polistinae that have been studied. Other species in the genus have been mentioned in the literature in this connection. Queens of *S. flavipennis,* for

Table IV. Degrees of Polymorphism in Social Wasps.

Species	Dimension used for body size	Average body size (mm) queens	workers	Ratio queen/ worker	Source
Polybia rejecta	mesonotum length	2.16	2.22	0.97	Richards & Richards 1951
P. occidentalis platycephala	mesonotum length	1.62	1.50	1.08	Richards & Richards 1951
Stelopolybia areata	alitrunk length	4.17	3.64	1.15	present study
Vespula germanica	thorax width	5.23	3.81	1.37	Blackith 1958
V. rufa	thorax width	4.80	3.59	1.34	Blackith 1958

example, figured by Evans and Eberhard (1970), have an enlarged petiole. Both of these species form large colonies. This is consistent with the conclusion of Richards and Richards (1951) that species which form larger colonies tend to have more distinctive queens.

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BEHAVIOR OF THE NORTH AMERICAN TERMITE *TENUIROSTRITERMES TENUIROSTRIS*,[1] WITH SPECIAL REFERENCE TO THE SOLDIER FRONTAL GLAND SECRETION, ITS CHEMICAL COMPOSITION, AND USE IN DEFENSE[2]

By W. L. Nutting,[3] M. S. Blum[4] and H. M. Fales[5]

Introduction

Tenuirostritermes is a small genus of Neotropical termites with two species ranging northward into warm temperate, semi-arid areas of southwestern Texas [*cinereus* (Buckley)] or beyond into southeastern Arizona [*tenuirostris* (Desneux)]. As a member of the Nasutitermitinae, it is somewhat more primitive than the very large and well-known tropicopolitan genus, *Nasutitermes*. The subfamily, containing the most highly specialized members of the Termitidae, is the largest in the order Isoptera. The major specialization within the subfamily has involved gradual reduction of the soldier mandibles to non-functional stubs with concomitant development of a small projection on the front of the head into a long, attenuated snout or nasus. The frontal gland, occupying most of the bulbous posterior of the head capsule, elaborates a defensive secretion which can be forcibly ejected through the frontal pore at the tip of the nasus by contraction of powerful mandibular muscles. This fontanellar gun represents the apex of sophistication among the varied chemical defense mechanisms of the termites. The zoogeography and affinities of the nasutitermitine genera have been discussed by Emerson (1955) and Krishna (1970) and their defensive behavior by Ernst (1959), Moore (1969) and Wilson (1971). Light and Weesner (1955)

[1]Termitidae, Nasutitermitinae.

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and Weesner (1953, 1970) have made the only major contributions on the general biology of *T. tenuirostris,* and Nutting (1970) has summarized the information on its foraging behavior.

Materials and Methods

Seven collections of the termites were made in early September, 1972, on the Santa Rita Experimental Range, elevation between 945 and 1220 m, ca. 45 km south of Tucson, Arizona. The area is a shrub-invaded desert grassland ecotone, characterized by scattered trees, shrubs and cacti. Four groups were taken from under stones during one afternoon and three nearly complete foraging groups were taken on the soil surface near midnight. Termites and a minimum of soil were quickly scooped up with a trowel and placed in a large enameled tray. A few hours later the termites were separated from soil and debris by sifting and hand-picking. To determine soldier/worker ratios, these castes were counted in each of the two combined collections, those from under stones, and those taken on the surface. Several hundred of these soldiers and workers were reserved for chemical analyses.

A small foraging group was collected later for behavioral studies. They were supplied with fine, dry native vegetation and survived reasonably well in the laboratory for about three weeks in a plastic petri dish of moist soil. A few minor workers of the myrmicine ant, *Pheidole desertorum* Wheeler, were also collected in the same area and maintained for the observation of termite-ant encounters. Although most species of *Pheidole* are reportedly seed gatherers rather than habitual predators, this was apparently of no consequence in the artificial situations described below.

No encounters between termite foraging groups and small arthropod predators were seen in the field. A few random encounters were staged in the laboratory by introducing individual ants into the dish containing the small group of termites. The defensive behavior of the soldiers was observed in detail under low magnifications of a stereomicroscope, during individual soldier-ant encounters contrived as follows: Single living ants were mounted in a natural position on glass slides with a small drop of rubber cement. Slide and ant were then placed on the soil in the observation chamber with the termites. In this distinctly one-sided situation, one or more soldiers invariably located and attacked the ant within a few minutes.

Attacks by five different soldiers were quite literally recorded on

separate slides in the form of discrete threads of frontal gland secretion which they had fired in the general direction of the ants. The volume of most of these shots was calculated from measurements made of the threads with an ocular micrometer under a compound microscope. Drawings to illustrate the variation of individual shot patterns were made with the aid of a camera lucida on the same microscope. The fate of a few ant victims was followed until their death and compared with that of normal ants which were isolated and allowed to die of starvation and desiccation.

For the chemical analyses 600 living soldiers were placed in reagent *n*-pentane. Although it had been determined that the heads of the soldiers were the primary source of the odorous defensive compounds, 400 living workers were also extracted for comparative purposes. The extracts were concentrated under vacuum and analyzed on a gas chromatograph interfaced to an LKB-9000 mass spectrometer. A 4-meter column of 10% SP-1000 on 80/100 mesh Supelcoport operated isothermally at 65°C was employed for all analyses.

Results

Foraging behavior. — *T. tenuirostris* forages in the open on the soil surface, mainly at night in southern Arizona as we have recently established, but it is also active on cloudy days, at least in western Mexico (Nutting, 1970). The following account of its general foraging behavior is a synthesis of observations made on about 12 different groups at the Santa Rita Experimental Range during September-October, 1972.

Workers presumably open one or more access holes to the surface, but the soldiers are generally the first out and the last to return underground during bouts of surface activity. As many as 100 or more soldiers and very few workers may congregate within a 5- to 10-cm radius of the hole prior to foraging. Little organization is at first apparent except that many of the soldiers may be standing on the alert with heads pointed peripherally. One or more discrete foraging columns eventually emerge from such unorganized, milling masses, perhaps after the soldiers are joined by a critical number of workers. Once in motion, columns up to six workers wide move quickly in an ant-like manner, and show very tight trail-following behavior. While soldiers move out with the workers, they eventually take up stations at 1- to 2-cm intervals on either side of, and ca. 1 cm

from, the worker traffic. Columns occasionally branch and have been observed as long as ca. 2 m.

Irregular craters of soil, up to 8 cm in diameter and 1 cm high, are often thrown up around the holes during periods of surface activity. Ground-level runways radiating from the hole may be bridged over to transform a crater into a rough pile of soil 2 to 3 cm high. Since individuals of this species are relatively small (length of soldier, 3.0 mm; of worker, 4.5 mm), access holes as large as 5 mm in diameter probably provide for efficient, emergency re-entry of large numbers of foragers in a very short time. Workers have been observed to close the exposed holes shortly after the conclusion of surface activity and, although a few soldiers remain in and around the hole during closure, none was ever left outside. The same holes are apparently used repeatedly, at least for periods of several weeks.

The high proportion of soldiers in the foraging groups indicates the relative importance of this caste in those species of termites which routinely forage on exposed trails. The four combined groups collected from colonies beneath stones contained 545 individuals with a soldier:worker ratio of 1:3.82 (20.7% soldiers). Three combined foraging groups contained 1,549 individuals with a soldier:worker ratio of 1:1.23 (44.9% soldiers). A single foraging group of 230, perhaps recently organized, had a ratio of 1 soldier to 0.40 worker (71.3% soldiers).

Soldier behavior. — Whenever the laboratory group of soldiers and workers was disturbed by jarring or removing the cover of their container, several soldiers, with antennae raised and waving, congregated on the edges of objects and on elevated vantage points. Individual workers of the ant, *Pheidole desertorum* (ca. 3.5 mm long), introduced into this situation were quickly fired on at very close range by several soldier termites in rapid succession. The appendages of such victims were almost completely immobilized, within 10 sec or less, by the viscous, glue-like threads thrown over them.

Further details of soldier defensive behavior are based on observations made during encounters with living ant workers fixed to glass slides. Although blind, the soldiers presumably orient toward such threats by olfactory or auditory cues. An alerted soldier closes rapidly on any potential target and may actually touch it for an instant with its antennae before firing — from a distance of ca. 0.5-3.0 mm). As it fires, it may jerk forward or backward, in position, and may or may not then oscillate to-and-fro one or more times. This apparently insignificant bit of behavior greatly enhances the effectiveness of the

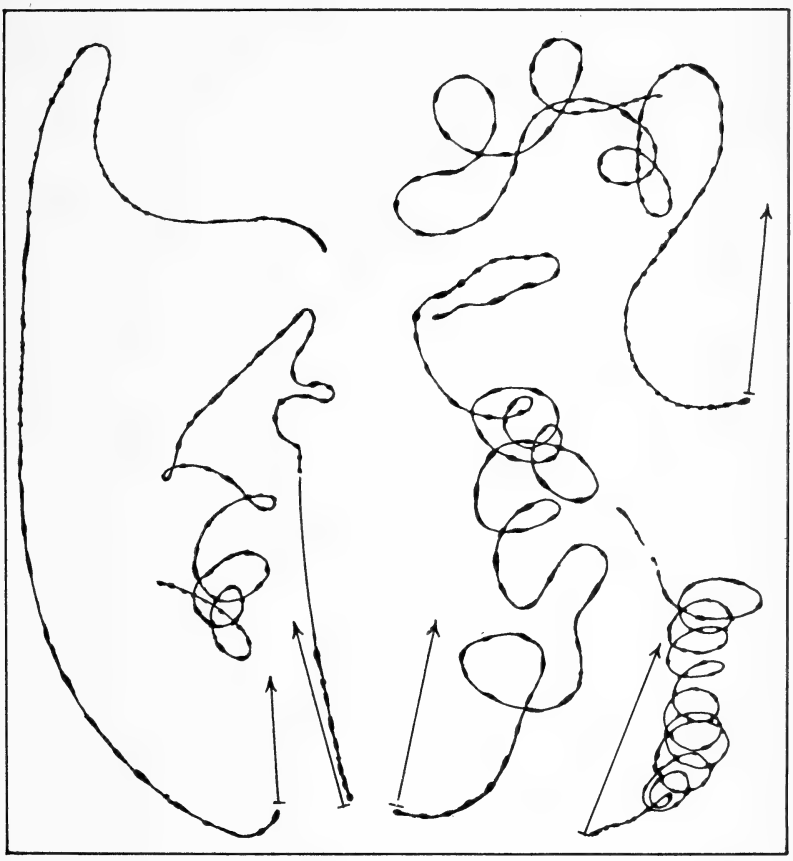

Fig. 1. Patterns of the threads of frontal gland secretion fired by five different soldiers of *Tenuirostritermes tenuirostris* at living ants fixed to glass slides. Arrows show direction of target and scale of 1 mm.

Table 1. Measurements of shots or threads fired by four soldiers of *Tenuirostritermes tenuirostris* at fixed, living ants in the laboratory.

Soldier Number	Shot Number	Av. Diameter (mm)	Length (mm)	Volume (mm^3)
1	1	0.020	19.650	0.0062
	2	0.015	11.425	0.0020
	3	0.015	10.475	0.0019
	4	0.015	7.550	0.0013
	5	0.015	5.100	0.0009
	6	0.015	2.500	0.0004
2	1	0.020	9.025	0.0028
	2	0.020	7.300	0.0023
3	1	0.020	7.200*	0.0023
	2	0.020	4.625	0.0015
	3	0.020	1.725	0.0005
4	1	*		
	2	0.020	0.900	0.0003

* Shot entirely on ant and not traceable, or partly on ant and measurement only approximate.

soldier's shot by throwing a bight, or even one or more loops, in the thread (Fig. 1). Attacks by as many as six soldiers from different directions were invariably fatal to an ant. Soldiers often examined victims with their antennae for up to a minute, occasionally becoming temporarily entangled themselves. They were never seen to wipe the nasus on the substrate after any of this activity.

In unstaged encounters, soldiers usually fired but once at an ant; however, by carefully prodding and exciting the fixed ants, individual soldiers were induced to fire from one to six additional shots at them. Data on the shots recorded on and near four such ants are summarized in Table 1. It was impossible to determine the order of shots fired by individual soldiers, but those of greater diameter and length are probably the ones fired at or near the beginning of an encounter. Longer shots often began with a series of droplets, and occasionally contained short breaks in the thread. It would have been interesting to determine what percent of their glandular holding capacity had been spent in these individuals, but drought conditions during seasons of activity have since prevented further collections.

Although the ant victims were physically immobilized within a few seconds, they also appeared to be adversely affected by some of the chemical components of the soldier secretion, probably the terpenes.

They lay very quiet, moving their appendages but little even when prodded. Their struggles were very feeble after 1.5 hr, while only occasional, slow contractions could be elicited after 4 hr. They appeared essentially dead after 5-6 hr. By comparison, normal ants, similarly confined without food or water, remained so for 5-10 hr, showed postural difficulties after 10-12 hr, responded vigorously to prodding for as long as 24 hr, and did not appear to be dead until 24-33 hr after confinement.

Chemical Analyses. — Three compounds accounted for over 90% of the low boiling volatile compounds which were detected in the extracts of the soldiers. Based on the congruencies of their gas-chromatographic retention times and mass spectra, the volatiles were identified as α-pinene, myrcene, and limonene. The mole percentages of the compounds were: α-pinene 62%, myrcene 27%, and limonene 11%. None of these monoterpene hydrocarbons was detected in the extracts of the workers.

Discussion

Ernst (1959) was inclined to believe that the frontal gland secretion of soldiers of a *Nasutitermes* sp. from the Ivory Coast was essentially non-toxic and that it functioned primarily to entangle its enemies. He did not rule out the possibility of an insecticidal effect. Considering that normal worker ants survived without food or water 4 to 6 times as long as those immobilized by the *T. tenuirostris* soldier secretion, we feel that the terpenoid components of its secretion are definitely toxic.

Ernst also observed that the secretion fired by one of his *Nasutitermes* soldiers stimulated nearby soldiers to fire, thus suggesting that it contains volatiles which act as an alarm pheromone. On the basis of his own work with several Australian species of *Nasutitermes,* Moore (1969) has suggested that α-pinene might serve as such a pheromone. This compound probably serves a similar function in *Trinervitermes geminatus* Wasmann (Nasutitermitinae) according to Quennedey (1973). Although we have not investigated this point, our observations suggest that any such alarm signal in the secretion of *T. tenuirostris* must act very briefly indeed. In a number of laboratory encounters between soldiers and free ants, several soldiers might fire once each on a single ant within a few seconds; however, late arrivals usually examined the resulting immobilized ants, but never fired on them.

Moore (1968) determined that both limonene and α-pinene were rather typical components of termitid soldier secretions whereas myrcene was detected only in one species of *Amitermes*. Vrkoč et al. have recently reported the major volatile components in the soldier frontal gland secretion of *Nasutitermes rippertii* to be α- and β-pinene and limonene, with myrcene among six minor constituents. Similarly, with *N. costalis* they found α- and β-pinene and limonene among six major constituents of the secretion, and myrcene again among three minor components. However, although it is evident that monoterpene hydrocarbons are rather characteristic defensive products of nasute soldiers, these compounds do not appear to have a widespread distribution in the Insecta. Indeed, with the exception of the myrmicine ant *Myrmicaria natalensis* F. Smith, which produces limonene in its poison gland (Grünanger et al., 1960), monoterpene hydrocarbons have not been identified in any other insect taxa.

By taking high speed motion pictures of *Nasutitermes* soldiers attacking vestigial-winged *Drosophila,* Ernst (1959) determined that they move rapidly forward and backward (only once?) in delivering the jet of frontal gland secretion. He also observed one soldier to move its head from side to side during an attack. Our tracings of the shot patterns (Fig. 1) show that either or both of these movements are also used by soldiers of *T. tenuirostris* to increase the effectiveness of their defense. The basic oscillatory behavior probably represents the jerking or rocking movements which termites commonly exhibit in mild alarm situations. We have also shown that soldiers are capable of firing more than once, if sufficiently alarmed, and certainly do not deliver the entire contents of the frontal gland in a single discharge as Ernst suggested.

Many authors have stated that ants are the chief predators of social insects, with the termites not the least among their prey (Wilson, 1971). There can be little doubt that the nasute soldier is a highly effective defender of the colony against arthropod predators close to the size range of the termites themselves. A large force of nasutes would seem to be of critical importance in protecting the workers on their food-gathering expeditions, particularly those that forage in the open as does *T. tenuirostris*. However, this common assumption apparently rests largely on casual, subjective observations and circumstantial evidence of the type presented here. Quantitative data required to prove this assumption are not available and would be extremely difficult to obtain.

The high proportion of soldiers maintained by *T. tenuirostris,* and presumably many other free-foraging termites, certainly attests to their great importance in the colony. Our figure of 20% soldiers in combined collections from four different colonies is in fair agreement with Light and Weesner (1955) who determined that incipient colonies of this species usually contained between 25 and 33% soldiers. Three of our foraging groups combined contained 44.9% soldiers, while a single group contained 71.3%. Ernst (1959) reported 70 to 90% soldiers in outer portions of his laboratory colony of *Nasutitermes* sp. from the Ivory Coast. Although demands on the defensive capabilities of the soldiers underground must be trivial or rare, indeed, these figures show that a very high proportion of soldiers is mobilized for foraging parties.

This situation is in striking contrast to that in another subterranean termitid, *Gnathamitermes perplexus* (Banks) (Amitermitinae), which is very common over the range of *T. tenuirostris* in southern Arizona. This species forages widely on the surface under cover of thin, soil sheeting which it builds over all types of dead plant material (Collins et al., 1973). Based on 74 foraging groups, the average soldier:worker ratio is 1:89 (1.11% soldiers). Individual groups ranged from 1 to 1031 termites and contained from 0.0 to 9.10% soldiers (Nutting and Haverty, unpublished).

During the few hours of field observations on the above-ground activities of *T. tenuirostris,* no encounters with ants or other small predators were seen. However, the presence of an impressive ant fauna in our study area lends further credibility to the importance of the soldier caste in the economy of this termite. In a preliminary study of the ants on the Santa Rita Experimental Range, Gaspar and Werner (unpublished) list 33 species, with high populations of *Crematogaster coarctata vermiculata* Emery and *Forelius foetidus* (Buckley), and estimate 1753 nests/ha for all species. About one fourth of the species are regular predators, while at least an additional third are occasional predators or at least feed on animal matter. Many of them forage at night during the summer rainy season when *Tenuirostritermes* is also most active on the surface. Although we have no estimates of colony size or density for the termite, its colonies are fairly common in the area and must contain several thousand individuals.

Acknowledgments

We wish to thank Dr. Ch. Gaspar, Laboratoire de Zoologie générale et de Faunistique, Faculté des Sciences Agronomiques de l'Etat, Gembloux, Belgium, for identifying the ant used for our laboratory observations, and Mr. Michael I. Haverty, Research Associate, Department of Entomology, University of Arizona, for his assistance in collecting the termites.

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THE CASTIANEIRINAE OF MEXICO. I. *CASTIANEIRA DUGESI* (BECKER) (ARANEAE: CLUBIONIDAE)*

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Since the revision of the Castianeirinae of North and Central America (Reiskind, 1969) new collections have been made and studied. This is the first of a series of papers that will update the Mexican component of this subfamily.

Castianeira dugesi (Becker) has been known from a single male described almost a century ago. Recent collections from locations within 50 miles of the type locality have produced additional specimens including the first females. *C. dugesi* is the nominal species in the *dugesi* species-group (which also includes *C. nanella* Gertsch and *C. alfa* Reiskind), a group restricted to the dry regions in southwestern U. S. and northwestern Mexico and characterized by its moderately small size, lack of plumose setae, and distinctive genitalia (Reiskind, 1969). As is characteristic of many ant mimicking species of *Castianeira* with no distinct morphological separation of cephalic from thoracic region the cephalic region in *C. dugesi* is marked off by color pattern which we can assume reflects the color pattern of the model ant.

Castianeira dugesi (Becker)
Figures 1-3

Micariaulax dugesii Becker, 1879, Ann. Soc. Entomol. Belgium, 22: 83, pl. 2, fig. 9, 10, ♂, from Guanajuato, Mexico; in the Brussels Museum.
Castianeira dugesii: Simon, 1897, Histoire Naturelle des Araignées 2(1): 167.
Castianeira dugesii: F. P.-Cambridge, 1899, Biol. Centrali-Americana. Arachnida 2: 81.
Castianeira dugesii: Reiskind, 1969, Bull. Mus. Comp. Zool. 138(5): 223-225, pl. 10, fig. 127, 128.

FEMALE

Measurements. Based on two females: carapace length 2.65-2.70 mm; carapace width 1.70-1.75 mm; carapace index (carapace width ÷ carapace length × 100) 64; sternum length 1.15 mm;

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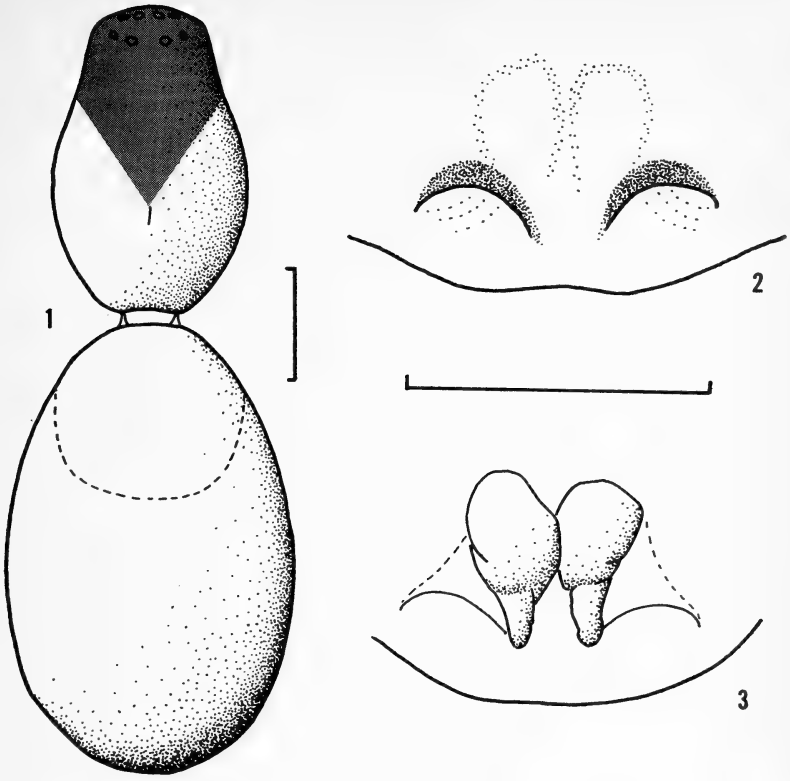

Figures 1-3. *Castianeira dugesi* (Becker). Fig. 1. Dorsal aspect of female. Pattern division of carapace shown by shading. (Vertical scale line = 1.0 mm) Fig. 2. External epigynum. Fig. 3. Internal epigynum, dorsal view. (Horizontal scale line for epigyma = 0.5 mm)

sternum width 0.95 mm; sternum index (width ÷ length × 100) 80.

Femur IV length 1.75-1.85 mm; femur IV width 0.45-0.55 mm; leg thickness index (femur IV width ÷ femur IV length × 100) 26-29; leg length index (femur IV length ÷ carapace length × 100) 67.

Abdomen length 4.00 mm; abdomen width 2.30-2.35 mm; abdomen index (width ÷ length × 100) 57-58.

Description. Carapace orange-brown and hairless, with cephalic region dark brown (Fig. 1). Carapace moderately narrow in head region (width at level of second eye row 0.59-0.61 times the maximum width of the carapace) and smoothly truncated anteriorly. Eyes moderately small, equal with posterior row somewhat wider than anterior. Distinct thoracic groove.

Abdomen oval, grey-brown, with a large anterior dorsal dark red-brown scutum (about one-third the length of the abdomen) (Fig. 1); covered with sparce, fine setae. Epigastric and small inframammiliary scuta red-brown. Both pairs of anterior abdominal setae hairlike.

Sternum orange-brown with light, thin setae.

Chelicerae dark-brown (like cephalic region of carapace) with two moderate retromargin teeth and two slightly larger promargin teeth. Pedipalps with red-brown femur and rest yellow.

Coxa I yellow-brown, rest of coxae yellow. A small notch on trochanter IV.

Femur I dark brown with yellow distal end, rest of leg I and leg II and III yellow; leg IV dark yellow with orange metatarsus. Tibia I ventral spination: 2 (prolateral)-2 (retrolateral) and small.

External genitalia with a pair of wide, flared openings (Fig. 2). Internal structure with globose spermathecae drawn out into narrow straight posterior necks (Fig. 3).

MALE

Measurements. Based on two males: carapace length 2.05 mm; carapace width 1.25-1.30 mm; carapace index 61-63; sternum length 0.95-1.00 mm; sternum width 0.75 mm; sternum index 73-77.

Femur IV length 1.40-1.45 mm; femur IV width 0.35 mm; leg thickness index 24-25; leg length index 69-71.

Abdomen length 2.45-2.60 mm; abdomen width 1.15 mm; abdomen index 45-47.

Embolus length 0.06-0.07 mm; genital bulb length 0.63-0.65 mm; male genital index (embolus length ÷ bulb length × 100) 9.5-10.

Description. Similar to female with the following differences: Only the anterior portion of carapace cephalic region dark-brown. Abdomen with a full scutum, granulose at anterior end and gradually becoming smooth and shiny posteriorly. Tibia I ventral spination: 1-0 and small. Genital bulb drawn out into a long neck ending with an embolus having a right angle near tip (illustrated in Reiskind, 1969).

Diagnosis. C. dugesi differs from other *dugesi* group members in its genitalia (right angle at end of male embolus and straight spermathecal necks), distinct patterns of carapace and legs.

Distribution. Apparently this species is restricted to a small region of central Mexico in northeastern Jalisco and Guanajuarto states.

Records. MEXICO. *Guanajuarto. Jallisco:* 10.8 mi. S. Talpa de Allende, 4900′, 8-VIII-67 (R. E. Leech); 13 mi. SE. Lagos de Moreno, 6450′, 7-IX-67 (R. E. Leech, G. E. Ball).

The female of *Castianeira dugesi* would key out to couplet #36 in the Key to the Females of *Castianeira* in Reiskind (1969). It can then be separated from the other species included in that couplet by its dark abdomen and bicolored carapace.

I wish to thank Dr. Robin E. Leech for the generous loan of the specimens studied in this paper.

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THE SOLDIER OF THE ANT *CAMPONOTUS (COLOBOPSIS) FRAXINICOLA* AS A TROPHIC CASTE*

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Complete dimorphism, defined as the coexistence of a minor worker of ordinary proportions with a larger major worker or "soldier," represents the pinnacle of the subcaste system within the ants. The soldier not only weighs more but also possesses a disproportionately larger head. By definition, intermediate forms are lacking. Complete dimorphism has originated independently at least seven times, within the following genera: the myrmicines *Pheidole, Oligomyrmex, Acanthomyrmex, Paracryptocerus;* the dolichoderine *Zatapinoma;* and the formicines *Camponotus* and *Pseudolasius.* The head shapes of the major workers of these groups are clearly modified either for fighting or for defense of the colony by blocking the nest entrances. These functions have been confirmed by direct observations of colonies of *Pheidole, Paracryptocerus,* and *Camponotus* (Wilson, 1971). The behavioral repertory of the major workers is otherwise very limited in comparison with that of the minor workers, giving logic to their alternate designation in the literature as soldiers.

The principal purpose of this article is to demonstrate that in at least one species, *Camponotus (Colobopsis) fraxinicola* M. R. Smith, the soldier caste also plays a key role in liquid food storage.

Materials and Methods

Colonies were collected at St. Mark's Lighthouse and Tall Timbers, near Tallahassee, Florida. The taxonomic identification requires a brief note. Three forms of the southeastern United States, *fraxinicola, impressus,* and *pylartes,* are very similar to each other and may prove synonymous. The Tallahassee series fall closest to *fraxinicola* in the seemingly best character states of the major worker: a slightly more flattened mesonotum, more rounded posterior rim of the truncated portion of the head, and in other, more subtle details of head shape. But all of these characters vary widely within and among series from widespread localities, so that eventually only one

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species might be recognizable, which would then take the name *impressus.*

The colonies were transferred to glass tubes 15 cm in length and 3-6 mm in inner diameter. The tubes were each plugged at one end with dry wads of cotton wool and placed in open plastic containers, the inner sides of which were lined with fluon to discourage climbing by the ants. Since the latter method does not always work with these highly arboreal ants, the containers were also supported by glass bottles set in petri dishes filled with heavy mineral oil. Water was made available in moistened cotton plugs at the bottom of test tubes placed next to the tubes housing the colonies. The ants were fed daily with honey and freshly killed insects. Entire colonies quickly habituated to strong light. They could be observed *in toto* with a swing-arm dissecting microscope without being disturbed in their new, highly simplified (and fluon-lined) universe.

The Soldier as a Defensive Caste

Since the time of Forel (1874) it has been known that soldiers of the subgenus *Colobopsis* of *Camponotus* use their oddly cylindrical heads to block the nest entrances. Minor workers returning from foraging trips identify themselves to the soldiers, presumably by colony odor. The soldiers then pull back to let them enter. *C. fraxinicola,* like most other *Colobopsis,* nest in the cavities of dead twigs. The nest entrances are neat, circular holes into which the heads of the soldiers fit snugly. By plugging glass tubes containing colonies with disks of cork, I was able to observe the excavation of the nest entrances on repeated occasions. The task was performed exclusively by the minor workers. This is somewhat surprising in view of the fact that the holes are cut to fit the specifications of the soldiers and not those of the minor workers. The soldiers also rested more consistently near the entrances of the glass tubes, with their heads pointing outward in a high proportion of cases, even when they were not actively engaged in blocking the entrances.

Undecane, stored in Dufour's gland of the abdomen, is a general formicine alarm pheromone (Wilson and Regnier, 1971). When small quantities of this substance were allowed to evaporate near the nest entrance, all members of the *fraxinicola* colonies were thrown into the typical excited running movements of the *fraxinicola* alarm response. But some of the soldiers moved to the nest entrances, filling those holes still unplugged at the start of the alarm reaction.

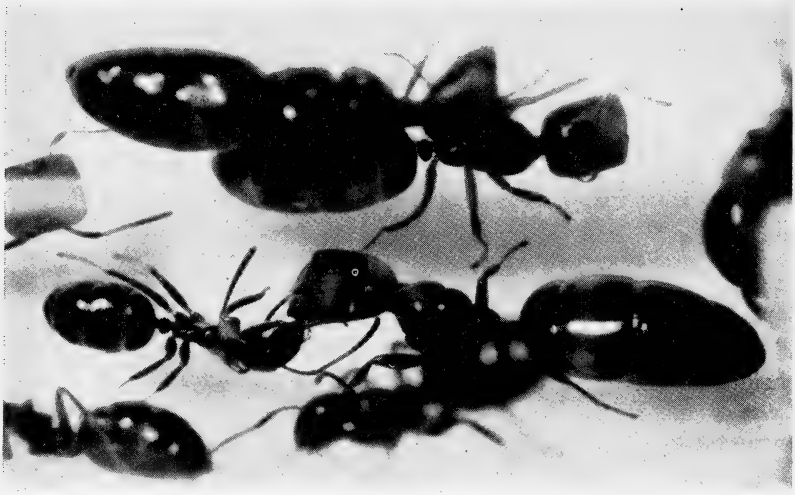

Figure 1. Portion of a laboratory colony of *Camponotus* (*Colobopsis*) *fraxinicola* housed in a glass tube. The large soldiers use their cylindrical heads to block the circular nest entrances, which are cut by the minor workers. This colony has been fed ad libitum, and consequently both soldiers and minor workers are in replete condition. In the center, a soldier and minor worker exchange food by regurgitation.

When twigs containing *fraxinicola* colonies are first broken open, both minor workers and soldiers rush out. Many attack any accessible alien object, such as the observer's hand or a bit of cloth offered to them, biting it and spraying it with formic acid. The same response was obtained in the laboratory by permitting fire ant workers (*Solenopsis invicta*) to invade the nests. Individuals of both castes were about equally aggressive and effective in repelling these invaders. On the other hand, the total population of minor workers, by virtue of its greater size, was more effective than that of the soldiers.

To sum up the results, the *fraxinicola* soldiers are indeed a defensive caste, but their specialization makes them superior in only one aspect of this role.

The Soldier as a Trophic Caste

The *fraxinicola* major worker is also anatomically distinguished by its proportionately larger abdomen. All individuals dissected from two laboratory colonies had large fat bodies and well developed ovaries containing one to seven eggs, some of which were of very

large size. A few minor workers with distended abdomens taken from within the nest had similar abdominal contents, but the majority from both within and outside the nest had proportionately much smaller fat bodies and reduced ovaries. Thus the soldiers store substantially more food in the form of fat than do the minors. The nature of their eggs has not been ascertained. Should they prove to be trophic eggs, this form of storage would be primarily the province of the soldier caste.

The following data reveal that the soldiers also store disproportionately large quantities of liquid food in their crops. When colonies are fed ad libitum with saturated sucrose solution or honey, most of the workers in both subcastes become repletes. Repletism has been defined for purposes of this analysis as distention of the abdomen to the extent that the intersegmented membranes are exposed, permitting the interior of the crop to be seen when light is transmitted from below. It has been repeatedly observed in our laboratory colonies that a higher proportion of the major workers — sometimes all of them — become repletes when the colony is offered a superabundance of liquid food. But when the colony is starved, the proportion of repletes among the majors drops below that of the minors. Two examples are presented in Figure 2.

The amount of liquid stored by each major is substantially greater than that stored by each minor, on both an absolute and per-unit-weight basis. This difference, which was first guessed by simple inspection, was proved by the following series of measurements. Twenty minors and 11 majors were selected at random and weighed from a colony anesthetized after two weeks of starvation. Then the colony was fed to satiety over a 24-hour period and anesthetized again; 20 minors and 16 majors were next selected at random from among the replete individuals and weighed. The mean weight of the starved minors was 1.62 mg (range 1.29-2.42 mg); after feeding, their mean weight was 2.44 mg (range 1.75-3.33 mg), a gain of 0.82 mg or 50.6 percent. The mean weight of the starved majors was 3.44 mg (range 2.38-4.65 mg); after feeding, their mean weight was 5.62 mg (3.14-7.34 mg), a gain of 2.18 mg or 63.4 percent.

The disparity in storage capacity can be seen even more clearly by examining the colony as a whole. The colony labelled No. 1 in Figure 2 can be taken as typical; it contained 139 minors, 26 majors, and a single queen. Using the data on weight gain and percentage of repletism during a single experimental run, the following storage capacities were estimated: the entire minor population stored 88.52

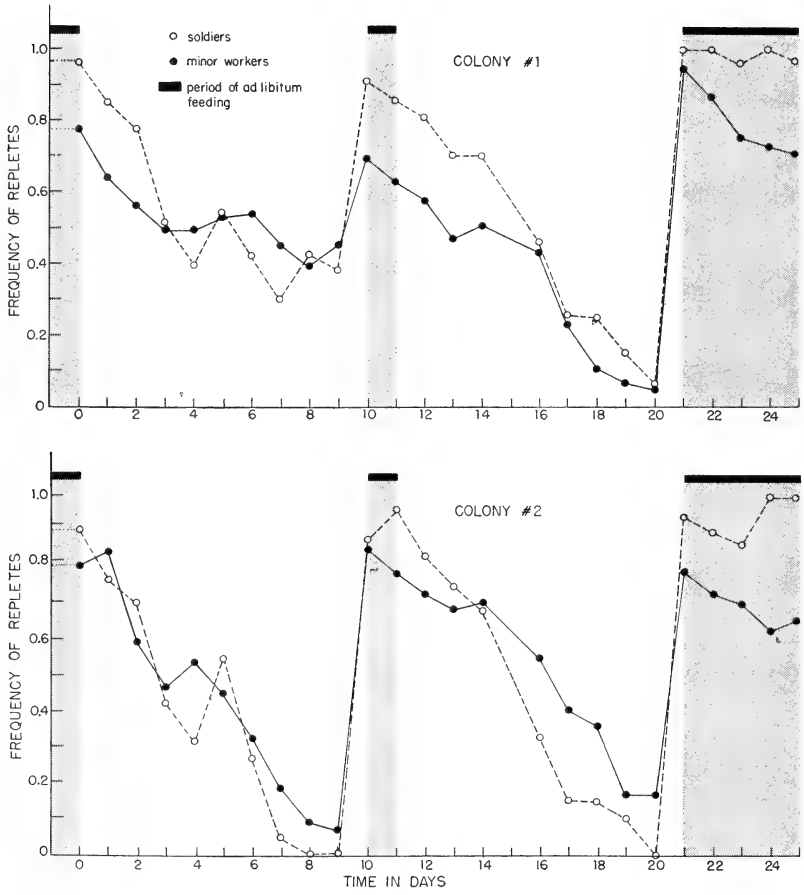

Figure 2. The frequency of repletes among the soldiers and the minor workers respectively in two colonies of *Camponotus* (*Colobopsis*) *fraxinicola*. The ants were fed to satiation with sucrose solution on three occasions ten days apart and starved in the intervening periods. The soldier caste consistently achieved a higher level of repletion when the colony was fed but surrendered it to a greater extent when the colony was starved.

mg, and the entire major population stored 54.59 mg. Thus although the majors made up a little less than 16 percent of the population and contained 28.43 percent of the wet weight in the non-replete condition, they stored 38.15 percent of the liquid at repletion.

A distinctive history of liquid flow unfolds when a colony discovers a single rich source of food and then endures a period of starvation — the circumstance simulated by the laboratory experiments. When the food is first discovered, the flow during the first one or two hours is from the foraging minor workers to other minors and majors encountered back at the nest. After saturation is attained, and 90 percent or more of the adults are replete, regurgitation continues at a high rate. The two castes participate at about the same per-worker rate, with no apparent difference between the majors and minors in the frequency of donation as opposed to that of reception. Within 2-3 days after the food is cut off, majors have begun to feed minors larger quantities than they receive. Data on exchanges show that the major-to-major donations are fewer than would be expected by chance alone. This is due at least in part to the fact that the majors are relatively sluggish in their movements. The minors are much the more active caste, passing from one nestmate to another to collect and pass along the dwindling supply of liquid food.

Acknowledgement

This article is part of a continuing study on caste systems supported by Grant Number GB-40247 from the National Science Foundation.

Summary

(1) The major worker, or "soldier," of *Camponotus* (*Colobopsis*) *fraxinicola,* helps to defend the nest by blocking the entrance holes with its head, a behavior pattern reported by previous authors in other members of the genus. However, when the nest is breached and combat ensues, the soldier is no more aggressive or effective than the minor worker.

(2) The nest entrances are constructed entirely by the minor workers, which cut them to fit the cylindrical heads of the majors.

(3) Major workers respond to undecane, a general formicine alarm substance, by moving to block those nest entrances still open at the beginning of the episode.

(4) Major workers also serve as a storage caste. Their abdomens are partially filled with exceptionally large fat bodies. They also store a disproportionate share of sugary liquids collected by the colony. When this food is superabundant, the majors reach a higher level of repletion. When the colony is subsequently starved, the majors regurgitate the liquid back to the rest of the colony faster than they receive it.

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CHEMICAL DEFENSE AND SOUND PRODUCTION IN AUSTRALIAN TENEBRIONID BEETLES (*ADELIUM* SPP.)*

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Introduction

Girdled eucalyptus trees, felled to make room for grazing pasture, are a common sight in rural Australia. In the dead and decaying stumps that are strewn through the countryside, many insects flourish. Two of these, the congeneric tenebrionid beetles *Adelium percatum* and *A. pustulosum* (subfamily Adeliinae) possess interesting defense mechanisms that we here describe. Both have eversible abdominal glands such as are commonly found in Tenebrionidae (Roth, 1945), but some features of the chemistry and biology of the glands are anomalous. Moreover, *A. pustulosum* has a stridulatory apparatus that may function for acoustical reinforcement of the chemical defense.

Materials and Methods

Both species of *Adelium* are black and, lacking hindwings, are flightless. Several dozen specimens were taken singly and in small groups in and under pieces of decaying eucalyptus wood in sheep pasture near Gudgenby, Australian Capital Territory, in mid-April, 1973 (Fig. 2). They were maintained in plastic containers, and given water, sucrose, and a variety of cereal-based foods. Initial behavioral and electronmicroscopic studies were done at the laboratories of the Division of Entomology, C. S. I. R. O., Canberra, where T. E. and M. E. were guests. Secretion was shipped to B. C. and J. M. for chemical analysis at the University of California, San Diego. Some beetles survived travel to Cornell, where acoustical studies were made by D. A., R. R. and T. E.

Scanning electronmicrographs were made with a JEOL (JSMU-UE) instrument. Preservation of beetles with everted glands was

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effected by first immersing them in cold (—195°C) liquid Freon (while held in forceps to cause eversion) and then transferring them to a tissue freeze-dryer for desiccation.

Instruments for chemical analyses included conventional gas chromatographs and an LKB-9000 gas chromatograph-mass spectrometer.

Sound recordings were made at 23-25°C with a condenser microphone from a Holgate Ultrasonic Receiver MK.V [frequency response ± 12 db from 1 to 100 kHz; sensitivity at preamplifier output 268 mv (rms)/μbar at 60 kHz (determined by substitution)], an Ithaco Amplifier Model 225 [variable amplification range from 0 to 80 db; flat frequency response (within 3 db) in range of 0.5 Hz to 100 kHz] and a Lockheed Magnetic Tape Recorder/Reproducer Model 419 [recording speed set at 30 inches/sec; flat frequency response (within 3 db) in range from 0.2 to 100 kHz; input sensitivity of 1.4 volt (1.0 volt rms) for ± 40% deviation]. Sound intensity was measured with a Brüell and Kjaer Precision Sound Level Meter Type 2203 and a Brüell and Kjar Condenser Microphone Cartridge Type 4145. The intensity measurements were limited to audio frequencies due to limitations in the frequency response of the Brüell and Kjaer Microphone [flat frequency response (within 2 db) in range from 2.6 Hz to 18.5 kHz].

Instruments used for displaying and recording temporal patterns of the sound included a Tektronix storage oscilloscope (Model 4103N) with differential amplifier (Model 5A22N) and Polaroid camera, and a Tektronix dual beam oscilloscope (Model 502A) with a Grass Kymograph camera (Model C4N). Timing marks were generated on the oscilloscope with a Hewlett-Packard function generator (Model 3310A).

Sound spectograms were made with a Kay Elemetrics Sonograph (Model 7029A). Low frequency background noise was filtered as needed during playback of the recordings with a Krohn-Hite filter (Model 3550).

Chemistry of the Secretion

It was clear from the outset that the secretion of both species was quinonoid in nature. The beetles responded typically to rough handling by protruding their glands, and the oily golden-brown fluid that visibly coated the everted structures had the unmistakable penetrating odor of benzoquinones, and the characteristic quinonoid

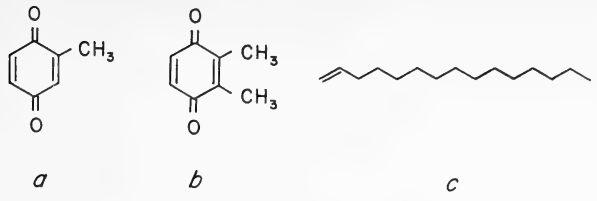

Fig. 1. Compounds in defensive secretion of *Adelium percatum* and *A. pustolosum*. *a;* 2-methyl-1,4-benzoquinone; *b;* 2,3-dimethyl-1,4-benzoquinone; *c;* 1-pentadecene.

property of tanning human skin. Our fingertips were always darkly mottled after handling a quantity of the beetles.

Secretion for analysis was obtained by seizing and squeezing individual beetles in forceps and wiping the fluid from the everted glands with small pieces of filter paper. The chemical procedure and the findings were the same for both species. Extraction of the papers with methylene chloride, followed by gas chromatography of the extract (1% OV-1 on Gas Chrom. Q, 4′ × ⅛″, 50° to 240°C), revealed the presence of three major components. Analysis by gas chromatography-mass spectrometry showed two of the components to have mass spectra identical to the published spectra (Budzikiewicz *et al.,* 1967) of 2-methyl-1,4-benzoquinone and 2,3-dimethyl-1,4-benzoquinone (Fig. 1 a, b). The third component had a mass spectrum matching that of 1-pentadecene (Stenhagen *et al.,* 1969) (Fig. 1 c). Definitive confirmation of the position of the double bond in this compound was obtained by ozonolysis. A small sample of the third component was collected from the gas chromatograph and dissolved in methylene chloride, and the cooled solution (−70°C) was subjected to a slow bubbled stream of ozone in oxygen until the blue color persisted. Addition of a small crystal of triphenylphosphine, followed by gas chromatography-mass spectrometry, showed the higher molecular weight product to have a mass spectrum identical to that of tetradecanal (Stenhagen *et al.,* 1969).

One interesting point in connection with these analyses was the observation of a fourth component in the initial sample of secretion obtained from both species. This component was guessed to be 1,2-dichloropentadecane on the basis of its mass spectrum, and the identification was confirmed by direct comparison of the isolated material with an authentic sample prepared by addition of chlorine to 1-pentadecene. However, since additional milkings taken from the same

beetles four months later into carbon disulfide rather than methylene chloride failed to show this component, it is apparent that the dihalide is an artifact derived from the olefin.

Structure and Defensive Operation of the Glands

Although the two beetles differ slightly in size and appearance — *A. percatum* is less rotund and longer (1.5-1.9 cm) than *A. pustulosum* (1.3-1.5 cm) — their glandular apparatuses are essentially identical. No dissections of fresh beetles were made, but judging from what could be discerned from specimens somewhat inadequately preserved in ethanol, the glands are anatomically similar in both species and probably homologous to eversible glands such as have been described for other tenebrionids (Lengerken, 1925; Roth, 1945; Tschinkel, 1972). Such glands are basically cuticular sacs, ordinarily withheld in inverted condition within the body cavity, and presumably everted by blood pressure. What is unusual about the *Adelium* glands is that they extrude to such great lengths. For example, gland length in a specimen of *A. percatum* 1.8 cm long that was freeze-dried with its glands everted, was recorded at 0.8 cm. Relative to body size, the glands of these beetles must rate among the largest eversible glands known for insects.

Examination of a glandular sac of *A. percatum,* treated with warm aqueous potassium hydroxide to remove all soft cellular parts, revealed a conventional membranous cuticular lining, with typical cuticular organelles attached (Fig. 8). Such organelles are a diagnostic feature of many insect gland cells (references in Eisner, 1970), and the ones of *Adelium* resemble closely those described from *cell type 1* in the defensive gland of the tenebrionid *Eleodes longicollis* (Eisner *et al.,* 1964). The organelles were distributed along the full length of the glandular sac, indicating that the secretory tissue is not restricted to a limited portion of the gland.

Gentle handling of *Adelium* usually induced no gland eversion at all. Only when the animals were more forcibly stimulated, as when they were grasped by the body or an appendage and squeezed, did

Figure 2. Pasture land near Gudgenby, A. C. T., Australia, where both species of *Adelium* were taken. Figs. 3-4. *Adelium percatum* responding to pinching of individual hindlegs by everting the gland of the side stimulated. Figs. 5-6. *A. percatum* responding to pinching of left midlegs. In Fig. 5 the gland has been maximally everted and has come into contact with the leg stimulated. In Fig. 6 the gland, on eversion, discharged part of its content as an anteriorly-directed spray (reference bar = 5mm).

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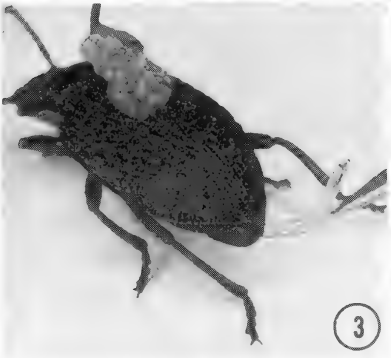
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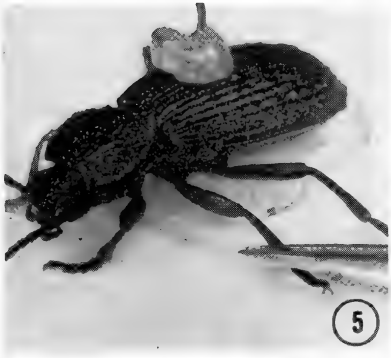
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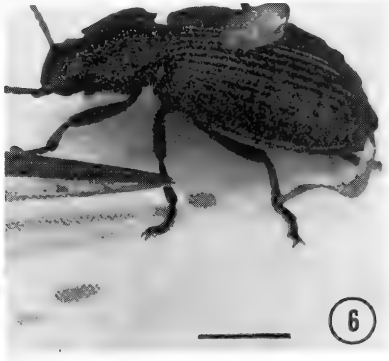
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eversion occur with some consistency. Reluctance to employ the glands in these animals is undoubtedly related to their possession of a particularly tough integument, which may in itself provide an effective first line of defense.

In order to observe more precisely the method of employ of the glands, individual *A. percatum* were affixed to wire tethers with wax, and stimulated by pinching their legs with forceps. The beetles were sometimes placed over filter paper impregnated with an acidified aqueous solution of potassium iodide and starch, a mixture that discolors darkly on exposure to benzoquinones (Roth, 1943) and provides a good visual means for detecting secretory emissions. The results were identical with all nine specimens tested. Stimulation of a single leg generally caused extrusion of only the gland of the corresponding side (Figs. 3-6). Simultaneous stimulation of two legs caused bilateral eversion. The extent and rapidity of extrusion varied, and seemed to depend on the intensity of stimulation. A brief squeeze of a hindleg or midleg, for example, usually induced only a partial eversion of the ipsilateral gland. Protracted or more vigorous squeezing elicited more complete and usually sustained eversion, and the extruded gland commonly extended outward far enough to contact the seized leg or forceps (Figs. 3-5). The target was usually visibly wetted by the gland. The beetles can apparently exercise some control over the direction of extrusion. Thus, when distal parts of a hindleg were stimulated, the gland usually extended outward at a greater angle relative to body axis than when more proximal parts of the leg were grasped. The gland is apparently aimed by flexion at its base rather than along its length, as evidenced by the fact that its shape is relatively fixed irrespective of its angle of protrusion.

When gland eversion occurred abruptly rather than gradually, as was generally the case in response to vigorous pinching, the sudden extension of the gland sometimes caused secretion to be ejected forcibly as a spray. (Figs. 6, 7). Ejections ranged from 1 to 5 cm, but in one instance droplets were shot to as far as 25 cm from the beetle. Forelegs and such other parts on the front of a beetle as are ordinarily inaccessible to the glands were inevitably doused by such ejections. Only beetles with replete or nearly replete glands tended to spray. However, animals with partly depleted glands could still effectively administer secretion to their front end. They did this by relaying secretion from one pair of legs to another, following initial wetting of the hindlegs by the glands. Even the antennae and the head itself were eventually wetted with secretion if they had been

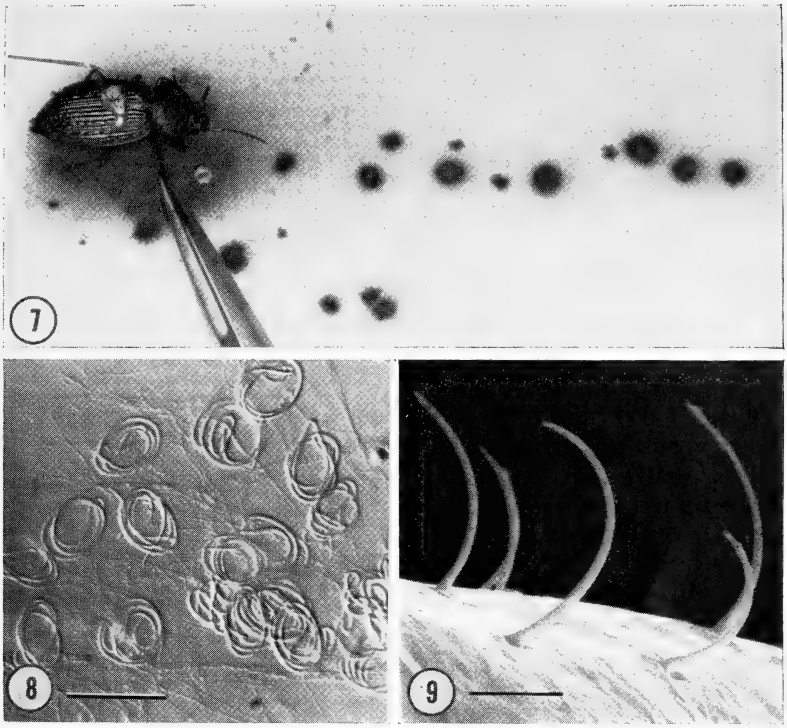


Fig. 7. Response of *Adelium percatum* to pinching of its right midleg. The animal everted its right gland abruptly, causing secretion to be sprayed forward. The droplets of secretion are shown as black spots on the indicator paper that served as substrate (filter paper impregnated with acidified aqueous solution of potassium iodide and starch). Far-ranging discharges as shown here occurred only when beetles had fully replete glands. Fig. 8. Cuticular organelles from secretory cells of gland of *A. percatum,* isolated by treatment of gland with warm 10% aqueous potassium hydroxide (Nomarski interference contrast; reference bar = 30μ). Fig. 9. Scanning electronmicrograph of hairs on exposed surface of everted gland of *A. percatum* (reference bar = 5μ).

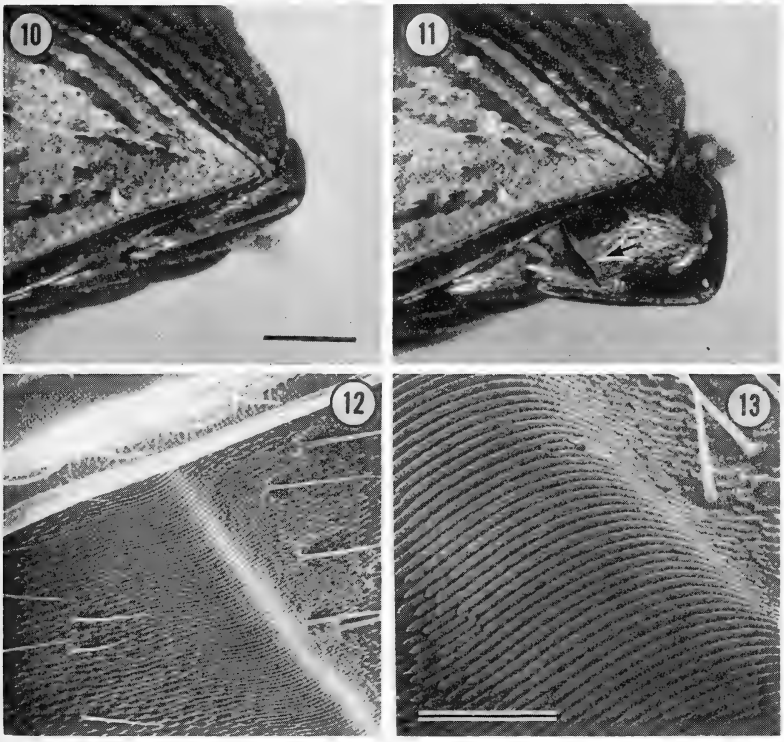
seized in forceps. The initial contact of hindlegs and glands appeared at times to be deliberate rather than fortuitous. Thus, when glands were insufficiently everted to effect automatic contact with the hindlegs, the legs sometimes reached back toward the glands and brushed against them. Wiping of midlegs against hindlegs, and of forelegs against midlegs, quickly followed. In cases where the beetles had been placed on indicator paper, the legs left dark markings on the substrate as evidence of their contamination. Some experiments comparable to the preceding were also done with *A. pustulosum,* with essentially similar results. However, forcible gland eversion with spray ejection was never seen in this species.

Scanning electronmicroscopic examination of the surface of everted glands of *A. percatum* revealed a covering of slender curved hairs (Fig. 9). Whether these are spaced closely enough to act as a matting remains uncertain. But it is conceivable that they function in this capacity, providing perhaps for the maintenance of uniform secretory wetness over the surface of the glands when they are everted and for spontaneous re-spreading of secretion over areas wiped clean by defensive action of the glands. Dispensation of secretion onto target surfaces might also be facilitated by the hairs.

Stridulatory Mechanism

When seized or pinched, *A. pustulosum* produced a distinctly audible sound. The response took precedence over gland eversion, and could persist for seconds if the disturbance was sustained. Two serrate ridges on the last (visible) abdominal tergite (Figs. 10-13) are responsible for engendering the sound. By rhythmic downward deflection of the abdominal tip — a motion depicted in Figs. 10 and 11 — the beetles scrape the ridges back and forth across the sharp overhanging elytral margins, thereby inducing a repetitive bi-syllabic chirp. Intensified stimulation eventually caused gland extrusion, which silenced the sound, since during gland eversion abdominal deflection is apparently precluded. *A. percatum* lacks the ridges and is soundless.

Stridulatory mechanisms are common in insects, and have been repeatedly noted. In the leaf-cutting ant, *Atta cehpalotes,* which produces sound by scraping a file in much the same manner as does *Adelium,* acoustical output and sound generation have been masterfully analyzed (Markl, 1968). Since this analysis is essentially applicable to *Adelium,* we will here describe only the properties of



Figs. 10-11. Dorsolateral view of rear of body of *Adelium pustulosum*, showing the abdominal tip in the undeflected (Fig. 10) and deflected (Fig. 11) positions that mark the limits of the stridulatory motion. The arrow points toward the left serrated ridge (reference bar = 1 mm). Figs. 12-13. Scanning electronmicrographs of the left stridulatory ridge. The elytral margin against which the ridge is scraped extends across the top of Fig. 12 (reference bar Fig. 13 = .05 mm).

the beetle's sound, without detailed consideration of the physical basis of sound production.

Only two live females and one male of *A. pustulosum* were available for sound studies. The animals were affixed to wire tethers glued to their pronotum with wax, and induced to stridulate by pinching their legs individually with forceps. Sound recordings were made with the beetles held at 1 cm from the microphone. An oscillogram of a typical chirp sequence is shown in Fig. 14A. The bi-syllabic composition of each chirp, indicative of the bi-directional movement of the ridges across the elytral margins, is clearly evident. Measurements made from oscillograms, of chirp repetition rates, chirp and syllable durations, and duration of inter-chirp and inter-syllable intervals, are summarized in Table 1, together with measurements of tooth counts and tooth spacings made from the serrate ridges. These parameters are evidently remarkably constant for any one beetle, although they differ somewhat between beetles. The Table does not give an indication of the gradual decline in the chirp repetition rate that characteristically took place with time following onset of pinching of a given leg (e.g. in a female, the rate declined from 2.25 to 1.63 chirps/sec over a period of 4.5 seconds). The decline occurred by a lengthening of the inter-chirp interval, rather than by prolongation of the syllables or inter-syllabic interval of the chirp itself. Accelerated chirping (or gland eversion) always occurred when pinching was shifted to a new leg or increased in intensity.

As was to be expected by analogy with the stridulatory chirps of *Atta,* and shown clearly by the oscillograms (Fig. 14B, C), the syllables are essentially trains of sound pulses, generated by impact of the elytral margins with the sequence of teeth on the ridges. Figs. 14D and 14E show oscillograms of individual pulses from a first and second syllable respectively.

Spectrograph analysis (Fig. 15) of the chirps revealed a frequency composition ranging broadly from below 1 kHz to 60 kHz. The frenquency distribution pattern was essentially similar in the first and second syllables, and differed little in spectrographs made with broad-band (Fig. 15 top) and narrow-band (Fig. 15 bottom) filters. Since broad-band filtration essentially analyzed the pulses one at a time, rather than in groups of three to five as in narrow-band filtration, it follows that the pulses themselves contain essentially the full range of the beetle's sound frequencies.

Apparatus for measuring sound intensities became available only after the beetles had died. Intensities therefore had to be measured

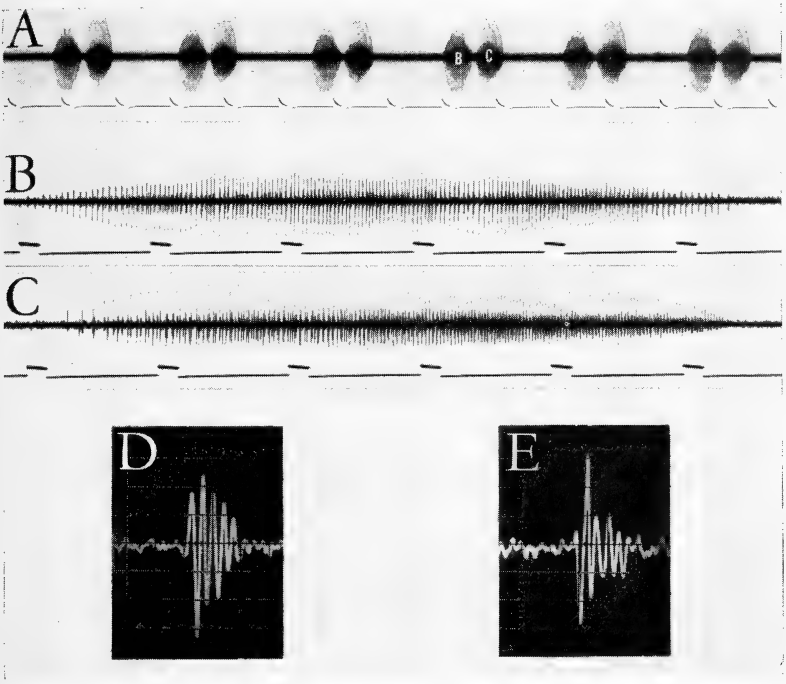


Fig. 14. Sound oscillograms of *Adelium pustulosum*. *A*, chirp sequence (2.8 sec. of ♀ no. 1); note bisyllabic composition of chirps (time interval = 200 msec). *B-C*, Expansion of the first (*B*) and second (*C*) syllables of chirp shown lettered in *A*; the pulsed nature of the sound is clearly resolved (time interval = 20 msec). *D-E*, Individual pulses of first (*D*) and second (*E*) syllables. (0.0625 msec/division).

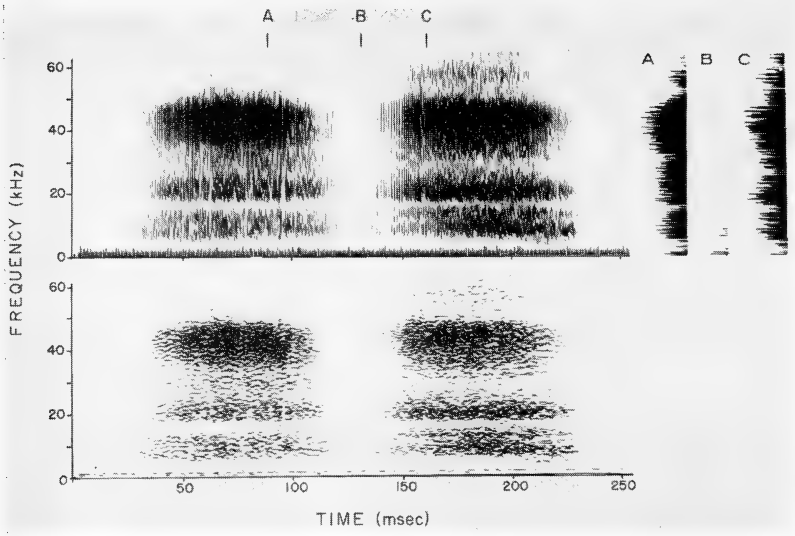


Fig. 15. Sound spectrograms of one chirp of *Adelium pustulosum* (the chirp is that lettered *BC* in Fig. 14*A*, and shown expanded in Fig. 14*B* and *C*). In each spectrogram the first syllable is on left and second syllable on right. Spectrograms were made from recorded sounds replayed at 1/8 speed. Top spectrogram: wide band analyzing filter (effective bandwidth 2400 Hz, with effective time response of 0.375 msec); bottom spectrogram: narrow band analyzing filter (effective bandwidth 360 Hz, with effective time response of 2.75 msec). Beside the top spectrogram are shown energy distribution profiles, corresponding to time transects lettered on the spectrogram itself.

indirectly, from the tape-recorded sounds of the beetles. This was done by monitoring the playback of the recordings with a microphone pickup and oscilloscope (the same microphone as used previously for recording of the chirps), and adusting the intensity of the playback until the induced oscilloscope signal matched that initially elicited by live beetles held 1 cm from the microphone. The intensity of the adjusted playback was then measured with the Sound Level Meter positioned at the site of the microphone, and found to be 65 db (relative to 0.0002 dynes/cm^2).

Detailed analysis of the oscillograms showed that the beetles apparently do not scrape both ridges with equal consistency during stridulation. In fact, stridulation appears to involve predominant scraping of only one ridge during downward deflection of the ab-

dominal tip (first syllable), and of both ridges with somewhat unequal force during the upward movement of the tip (second syllable). This conclusion rests on the observation that the syllables contain, in addition to a consistent major pulse (which in total number per syllable corresponds to the number of teeth per length of file estimated to be scraped during a syllable)[1], a subsidiary pulse of varying lesser amplitude, which appears sporadically in the first syllable, and fairly consistently in the second syllable. These lesser pulses, when they appear, result in a doubling of the pulse repetition rate. Moreover they bear a shifting rather than fixed temporal relationship to the primary pulses, suggesting that they are not subsidiary acoustical concomitants of single tooth scrapings, but a consequence of scraping of a second set of teeth of somewhat unmatched spacing relative to the first. The near absence of secondary pulses in the first syllable suggests that the beetle might not press the abdominal tip as vigorously against the elytral margins during downward abdominal deflection as during the return motion.

Discussion

Defensive glands that produce quinones are widespread among arthropods. They have been reported not only from other Tenebrionidae (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970), but also from certain termites (Moore, 1968), earwigs (Eisner and Blumberg, 1959; Schildknecht and Weis, 1960), cockroaches (Roth and Stay, 1958), grasshoppers (Eisner *et al.*, 1971a), carabid beetles (Aneshansley *et al.*, 1969; references in Moore and Wallbank, 1968; Schildknecht *et al.*, 1968), staphylinid beetles (Blum *et al.*, 1971; Brand *et al.*, 1973), millipedes (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970) and opilionids (Fieser and Ardao, 1956; Eisner *et al.*, 1971b). As is often the case with arthropod defenses, they exist as close counterparts in plants: glandular hairs that secrete a benzoquinone have been described for *Primula obconica* (Schildknecht *et al.*, 1967). Contrary to claim (Schildknecht *et al.*, 1964), not all Tenebrionidae

[1]From photographs such as Figs. 10 and 11, which depict the motion of the abdominal tip during chirping, it was estimated that this motion has a maximum amplitude of *ca.* 2/3 the length of a serrated ridge. This corresponds to about 130 teeth, a figure in line with the counted maxima of major pulses in the syllables.

have defensive glands (e.g., Tentyriinae and Asidinae). But the glands are frequently present, and when they are, they are either exclusively abdominal as in *Adelium,* or supplemented by a second pair of glands in the prothorax (Roth, 1945; Tschinkel, 1969).

Only relatively few tenebrionid secretions have been studied chemically. Most produce benzoquinones, including *p*-benzoquinone, and its alkylated derivatives 2-methyl-1,4-benzoquinone and 2-ethyl-1,4-benzoquinone (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970). Naphthoquinones have been reported in one species (Tschinkel, 1972) and in another the prothoracic glands produce phenols instead of quinones (Tschinkel, 1969). 2,3-Dimethyl-1,4-benzoquinone itself has not been found in a tenebrionid secretion, but it is produced by the defensive glands of certain opilionids (Fieser and Ardao, 1956; Eisner *et al.,* 1971b). The presence of an alkene in *Adelium* is no novelty. Hydrocarbons, both saturated and unsaturated, are known from arthropod secretions, and although 1-pentadecene as such has not been reported, shorter chain homologs of the substance are present in Tenebrionidae (Hurst *et al.,* 1964).

We made no effort to evaluate the defensive effectiveness of the secretion of *Adelium.* However, judging from the proven deterrency of other quinonoid mixtures to predators (references in Eisner, 1970, 1972; Eisner and Meinwald 1966), there can be no doubt that the glands of *Adelium* are protective in function. The presence of the alkene may be of more than incidental significance. It has been argued (Blum and Crain, 1961), and in one case proven (Eisner *et al.,* 1961), that lipoidal additives promote spreading and penetration of defensive secretions on target.

Defensive glands of arthropods vary greatly in structure and operation, and several characteristic types have been recognized (Eisner, 1970). The glands of *Adelium* appear to combine features of two of these types. Basically, by virtue of their extrusibility, they clasify as conventional *eversible* glands, but since they occasionally eject their

Table 1. *Adelium pustulosum:* Temporal characteristics of the chirps and morphological features of the stridulatory ridges. Temporal measurements were made from oscillograms and are given as mean ± standard error; sample size (N) is given in parenthesis. Morphological measurements were made from microscopic preparations of the last abdominal tergite of the beetles; tooth spacing was calculated by dividing ridge length by tooth number. (The tergite of ♀ no. 1 was damaged in preparation, hence the omission of measurements from one ridge.)

Table 1

Beetle No.	Chirp Rate (chirps/sec)	Duration (msec) of:				
		Entire Chirp	Interchirp Interval	1st Syllable	2nd Syllable	Intersyllabic Interval
1 ♀	1.96 ± 0.07 (15)	219.9 ± 3.9 (16)	290.0 ± 17.5 (15)	102.6 ± 1.4 (16)	97.6 ± 3.1 (16)	19.6 ± 1.1 (16)
2 ♀	2.26 ± 0.05 (26)	276.6 ± 6.1 (31)	161.0 ± 12.6 (26)	82.4 ± 3.4 (31)	123.4 ± 4.4 (31)	71.2 ± 4.0 (31)
3 ♂	2.66 ± 0.10 (26)	274.9 ± 4.8 (27)	99.4 ± 11.7 (26)	119.7 ± 2.6 (27)	130.0 ± 3.7 (27)	25.3 ± 0.8 (27)

Beetle No.	No. and Spacing (μ) of Teeth of Left (L) and Right (R) ridges			
	No. (L)	Spacing (L)	No. (R)	Spacing (R)
1 ♀	—	—	205	3.8
2 ♀	195	3.8	185	4.0
3 ♂	190	3.8	180	3.9

contents, they also qualify as *spraying* glands. We know of no other tenebrionid glands that operate in this way. Eversible glands are common, but they are generally shorter than those of *Adelium* and do not eject spray on extrusion. Spraying does occur, but only from non-eversible glands, as in *Eleodes* (Eisner, 1966). The peculiar habit of *Adelium* of relaying secretion by way of its appendages is not unique. Other tenebrionids are also said to use their legs for administration of secretion (Tschinkel, 1972), and comparable behavior has been reported for opilionids (Eisner *et al.,* 1971b) and Hemiptera (Remold, 1962).

Many insects produce chirps or other "disturbance" calls when they are molested. Cerambycid beetles, for example, very generally show this property, as do other beetles, cockroaches, Hemiptera, adult and immature Lepidoptera, and members of most other groups, including non-insectan arthropods (references in Alexander, 1967; Haskell, 1961; Roth and Hartman, 1967; Tuxen, 1967). The sounds are generally believed to be defensive, but it is by no means clear how precisely they act in this capacity. Convincing evidence has been advanced to account for the function of the calls in arctiid moths. These insects are chemically protected (Bisset *et al.,* 1960) and hence presumably distasteful, and they emit sounds, rich in ultrasound, in response to the echolocating chirps of bats (Blest *et al.,* 1963). Bats turn away from the calls, presumably because they have learned on the basis of previous experience with the moths that a prospective meal that "protests" audibly is distasteful (Dunning and Roeder, 1965; Roeder, 1967). The sounds, then, act as acoustical aposematic signals, operative in the dark just as visual aposematic adornments supposedly operate in the light. Defensive calls generally, to the extent that they are produced by chemically or otherwise protected insects and induced by encounters with predators, may function in this way. They might certainly do so in *Adelium pustulosum,* a furtive animal most likely to meet its enemies in darkness. But the calls need not only serve for acoustical reinforcement of a concomitant defense. They could also be intrinsically deterrent to predators, perhaps only to some, or they might function socially — as do "alarm" sounds in termites and ants (Howse, 1964; Markl, 1967, 1969; Markl and Fuchs, 1972) — to alert conspecifics to states of emergency. But these possibilities, like so many other functional suggestions that have been advanced for disturbance calls, remain to be proven. One wonders what predators might be affected by the chirps of *Adelium,* although criteria for compiling a list of enemies are lack-

ing. It seems clear, however, that the chirps are of sufficiently broad frequency composition to be at least potentially audible to virtually any acoustically sensitive predator.

Summary

The black flightless tenebrionid beetles *Adelium percatum* and *A. pustulosum* from Australia possess a pair of eversible abdominal glands that secrete a mixture of 2-methyl-1,4-benzoquinone, 2,3-dimethyl-1,4-benzoquinone, and 1-pentadecene. The tubular glands are unusually large, and when everted may be nearly half as long as the beetles themselves. In *A. percatum,* the replete glands may, on extrusion, spray their contents forcibly, to a recorded maximum distance of 25 cm. Defensive administration of secretion is also effected by the beetles' legs. *A. pustulosum,* unlike *A. percatum,* produces an audible "disturbance sound" when molested. The sound is engendered by the scraping of two serrated ridges on the last abdominal tergum across the elytral margins. The morphology of the stridulatory apparatus, and the acoustical properties of the sound, which contains frequencies ranging from below 1 kHz to 60 kHz, are presented. It is argued that disturbance sounds, when produced by chemically or otherwise protected animals, act as acoustical aposematic signals, operative primarily in darkness.

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SYNCHRONOUS VISUALIZATION OF VIDEO-TAPED SOUNDS AND MOTIONS OF INSECTS

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High-speed cinematography with synchronized oscillography has been used to analyze accurately the sound production by a rapidly moving structure during communicative behavior of insects (Walker & Dew, 1972; Willey, 1973, 1974). However, this method involves expensive equipment and perhaps kilometers of film containing only a few hundred feet of analyzable sequences. Nevertheless, the accuracy and resolution of audio-visual synchrony by this method has been exceeded only by the use of minute magnetometers using the Hall-effect (Elsner, 1970; Elsner & Huber, 1973) and by an ingenious method of flash-photography (Morris & Pipher, 1972). On the other hand, studies needing an average synchrony accuracy of only ± 5 msec (essentially equivalent to motion picture framing rates of 60 pictures per sec) can utilize inexpensive or already available video-systems used commonly as educational tools.

Video has several advantages over cinematographic methods: 1) sound and picture are routinely recorded synchronously, 2) videotape can be erased and reused, 3) some video-cameras have great sensitivity and can be used even for nocturnal insects at very low light levels, and 4) the system can be used to monitor behavior for hours and then sequences can be selected, duplicated on another tape and then the original tape can be used again. There are disadvantages of video for high resolution work and these will be discussed in the Analysis (q.v.).

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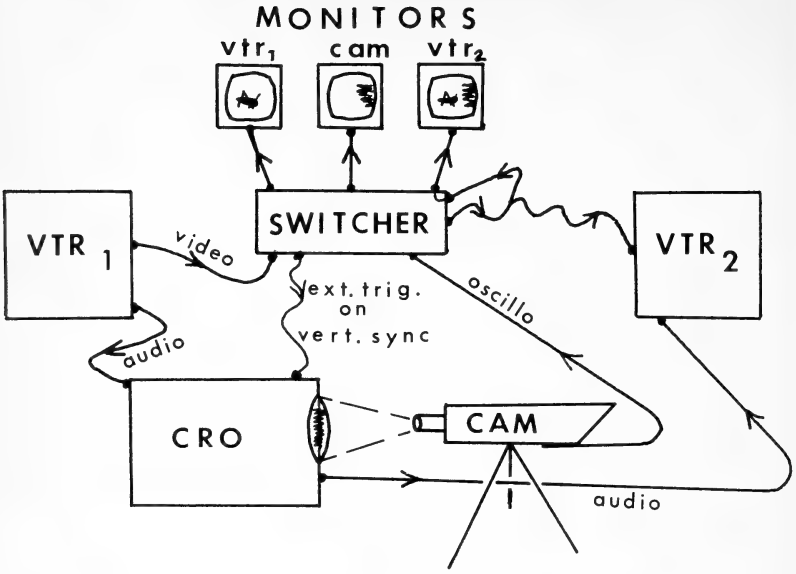


Fig. 1. Block schematic diagram of the equipment connected for line-by-line synchronization of a video field with a simultaneous full sweep of the cathode ray gun of the oscilloscope. The CRO is laid on its side so that the horizontal sweep passes from top to bottom of the superimposed field in VTR_2 (see text, sect. 8, Analysis). For ordinary horizontal sweep, the CRO is in normal position and the external trigger on the vertical sync is disconnected.

It seems strange that, with the exception of publications from our laboratory (Steinberg & Conant, 1974; Steinberg & Willey, 1974), we have found only a few studies of insect behavior which have involved the analysis of video-taped sounds and motion (Loher & Chandrashekaran, 1970, 1972; Hoeg-Guldberg, 1972). Moreover, even these studies have neglected to capitalize on the audio-recording and electronic potential of the video-tape system. We have devised a simple method to superimpose the oscillographic trace of the sound already recorded on any pre-existing video-tape on a duplicate recording. Extensions of this method to synchronous oscillography transduced from any mode will make video monitoring of insect behavior amenable to more versatile and precise analysis.

Method

A sequence was video-recorded with the following sound-related

parameters noted: 1) distance from the microphone to the subect, and 2) the average temperature of air between subject and microphone. Then we played the recorded sequence on a compatible video-tape reproducer (VTR_1) which was linked by a multichannel synchronizing circuit (SWITCHER) to another video-recorder (VTR_2) which preferably used at least one-inch tape. Figure 1 diagrams the set-up schematically. The audio circuit of the VTR_1 was linked also to the input of an oscilloscope (CRO), the screen (CRT) of which has an image persistence on the order of microseconds (P11 phosphor coating). A video-camera (CAM) focused on the CRT image which was positioned so that it would not mask the image of the subject in the superposition. If the trace was to be positioned along the bottom of the frame, the horizontal sweep of the CRO was set at 10 msec/cm so that a single sweep of 12.5 cm will encompass at least eight video fields (q. v., sect. 7 & 8, Analysis and Fig. 1 for further explanation and an alternative method). We also masked the negative potentials with opaque tape. The video-camera is connected with the VTR_2 by the vertical interval switcher and the CRT screen is shielded by an improvised hood from the room lights. The results of superposition are simultaneously video-monitored.[3]

The resulting video-tape, minus all the inactive time, can be played on a VTR which has stop-action and single-field forwarding capability (or the tape can be moved forward by hand). The audio signal can still be heard as well as seen as an oscillo-trace when the VTR is running at normal speed. At low speed the audio circuit automatically turns off and, although an adustment can be made in the machine's circuitry to enable the sound to be heard, with the oscillographic trace this is neither necessary nor desirable. With the VTR stopped on a single field, we marked with a wax crayon the positions of the moving parts on the projection screen of the monitor and made measurements of the angle changes with a protractor (a better method will be outlined later in section 9, Analysis).

[3]Equipment used: "Quiet Room" (Suttle, Inc., Chicago), Audiometric Room, double-walled (Industrial Acoustics, New York), Sony EV-310 25 mm videocorder, Scotch Brand MT 20568 video-tape, General Electric model 4TE33D1 TV camera with a Soligor 10 cm lens, Sony AVC 3200 TV camera with Angenieux 7.5 cm lens with a +1 diopter auxiliary lens, AKG shotgun microphone model D900, vertical interval switcher-sync generator with sync lock capability (Shintron 360), Tektronix 502A oscilloscope with P11 phosphor, Panasonic video-monitors (3-inch), one 50W electric spot bulb.

Analysis

Analysis of audio-visual synchrony must consider the following factors:

1) A video *field* is scanned from top of the screen to the bottom once in 16.67 msec at a maximum resolution of 262.5 lines per field; the horizontal sweep time for a line is 0.0635 msec. The vertical blanking interval (retrace time for the electron-gun to move from bottom of the screen to the top) requires up to 21 lines, and subtracted from the maximum resolution leaves a net resolution of 241.5 lines per field with a net duration of 15.5 msec, and a vertical blanking interval of 1 to 1.2 msec.

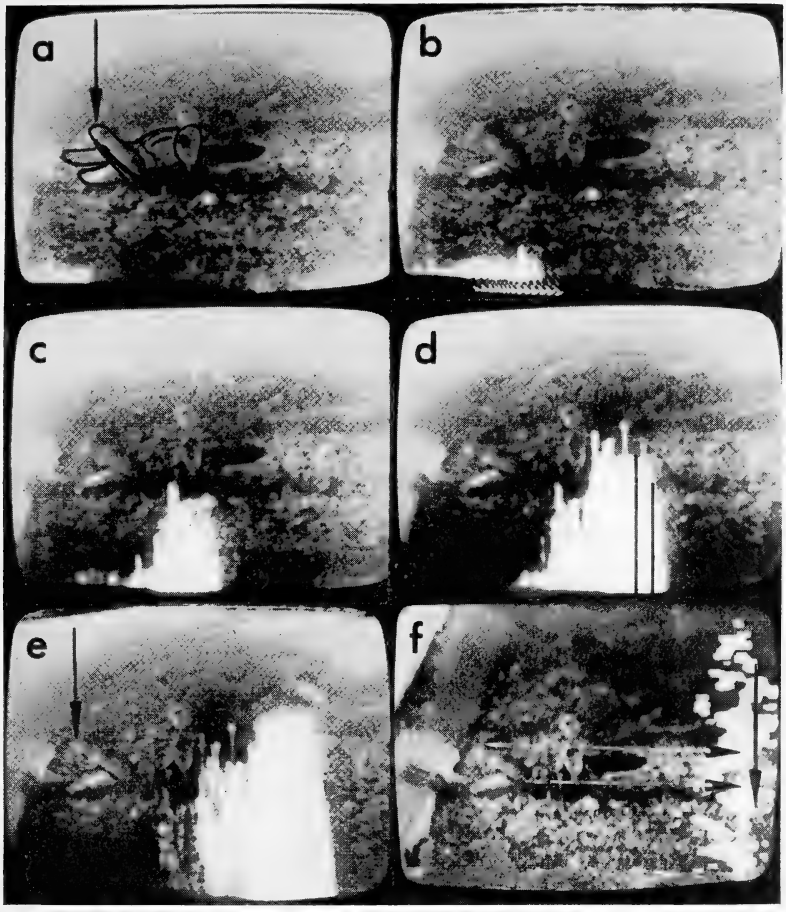
2) A video *frame* consists of two interdigitating video fields with a total net duration of 31 msec and a total net resolution of 483 lines.

3) Transduction of light and electronic impulses can be regarded as instantaneous, however the speed of sound in air is a variable. Near sea level, at 37 C and no greater than 10 cm from the microphone, one can calculate that the maximum time interval between sound production and electronic transduction is no greater than 0.4 msec and can be neglected as an important factor.

4) A crucial discrepancy in visual-acoustic synchrony and visual analysis of movements is the time taken by the electron-gun of the video camera to trace any action within a field. This factor causes three time-related distortions in the image which must be considered in the analysis, namely (a) vertical loss of resolution, (b) excessive curvature of a rotating image, and (c) inability to record events which occur after a scanning trace has passed until the next field scan.

5) Vertical loss of resolution: the image formed during a single field has a maximum vertical resolution of only 241.5 lines per field whereas a 16 mm optical-film frame has 50-60 lines of resolution per mm (at the center) or about 700 to 800 lines of resolution overall (allowing for loss of about 20 lines of resolution at the front and rear edge of the frame). On the other hand, the horizontal resolution of a good video system probably approaches that of a comparable optical-film system. However evaluation of information content of a video field and an optical film frame encompassing 15 msec is obscured by the next considerations.

6) Excessive curvature of rotating image: the time required for scanning a single field naturally produces a distorted image in any movement having lateral components. Plate 1a-e illustrates this



Pl. 1. A portion of a stridulation (chirp) by *Chortophaga viridifasciata,* showing a pulse of sound in five photographs of consecutive fields (a-e). The male which is chirping is outlined in (a), (b) and (c) show the right femur blurred as it makes the downward stroke (left femur is missing). The two vertical black lines drawn on the trace in (d) bracket the portion of the oscillotrace which was scanned at the time the leg was moving in this field. To the right of the lines is the base of a trace which really was much higher, but its peaks will not be scanned until the next field (e). The image persistence is due to retention by the video-camera pick-up tube and is about equal to one field ($\doteq$ 16 msec). The image in (f) is the result of triggering and synchronizing the CRT sweep with the "front porch" of the vertical field (set up as in Fig. 1). The field is identical to (e), but only the most intense peaks were registered. (See text, sect. 8)

problem with the oscillographic trace and a barely detectable clockwise curvature of the femur tip relative to the base in 1b and 1c. This is caused by the fact that a video field is a metachronic series of 241.5 lines each representing a "shutter speed" of 1/15,750 sec. The scanning time of the femur image in Pl. 1a is about 45 lines of 2.86 msec. In other words, the tip of the femur, which is moving in an arc to the left, is imaged nearly 3 msec earlier than that of the femur base. Further magnification on the screen would result in greater temporal displacements and greater artifact in the shape of the organ. Any attempt to measure angles of rotation or points of displacement must take into account the video scanning time of the specific image and its vector relative to the vertical trace.

7) Inability to record events after passage of the scanning trace: it is usually desirable to superpose the oscillotrace along the bottom of the video field (Pl. 1a-e) where the action is less likely to be obscured. However, the lower portion of the field will be scanned milliseconds after the action in the center. Nevertheless, visual-acoustic synchrony can be computed as shown in Pl. 1d. The selection of the horizontal sweep setting of the CRO is determined by the duration of the longest acoustical signal and should be about 40 or 50 msec longer, so that the oscillotrace of the entire action can be visualized in one sweep, and traces in successive frames can be cross-referenced. The additional time allows some time before and after the signal on the screen so that the beginning or the end of the signal and its causative motion aren't lost in the CRT retrace time, the vertical blanking interval, nor at the sometimes distorted edges of the monitor screen. Sometimes traces are badly reproduced or oriented, but constant inspection of the VTR_2 monitor will allow such mistakes to be corrected immediately by duplicating the sequence again.

8) An alternative method to achieve visualization of motion-sound synchrony is shown in Fig. 1 and Pl. 1f. Here the CRO is laid on its side so the oscillotrace will sweep from top to bottom of the camera pickup tube. The external trigger of the CRT electron-gun is triggered on the electronic transition from the vertical sync to the start of the first horizontal scanning line of the video field. The horizonal sweep of the CRT is set to equal the time constant of the video field (15 msec per sweep or 1 cm/msec), thus only the sound recorded during the video scan will be oscillographed. The oscillotrace peaks appearing at the same horizontal plane as the video-recorded movement will be relatively synchronous with that movement, with

allowance for the time lag induced by the speed of the original sound in air (Pl. 1f, arrows).

9) Close examination of CRTs can be a health hazard and the thickness of the protective cover can induce parallax error. Therefore, if exact angle and displacement measurements are desired the fields should be photographed with careful focussing on the video lines. Such photographs will form a permanent working record of key fields of the rather fragile video-tape which can be damaged or destroyed by the constant friction of scanning in the stopped position.

Discussion and Conclusions

This method allows relatively synchronous visualization of motions and the sounds produced by the movements if the actions are relatively slow. For example, it is possible to determine whether the stridulation by a single up-down motion of a grasshopper's hind femur rubbing against the fore-wing is produced during the up-stroke or down-stroke, provided the entire motion has a duration of >60 msec. In the case of oedipodine grasshoppers, the chirps produced by males during courtship usually are produced by motions which last at least 60 msec and often 100 msec (Willey, 1974). Since many such signals are complicated by being segmented into pulses within a single up-down motion, normal-speed cinematographic and audiospectrographic investigations of Oedipodinae (Otte, 1970; Willey & Willey, 1969) have concluded that the first pulse must be produced on the up-stroke. However, high-speed motion analysis (Willey, 1974) shows that *Arphia sulphurea* produces the definitive chirp on the downstroke only. A very weak signal was produced on the up-stroke but was of such low amplitude that it had never been audiospectrographed. Video-tapes of *Chimarocephala* (Loher & Chandrashekaran, 1970) and *Chortophaga* (Steinberg & Willey, 1974) also show that stridulations are produced only on the downstroke of the femur in these species. However, the mechanism for production of two-pulsed chirps must be analyzed by the higher speed methods (Willey, 1974).

Further refinements of this system can involve direct synchrony of oscillotrace with the initial video-tape recording. Also the use of a light-emitting diode (LED) and a small high speed digital clock in the background, synchronized with each video field, would simplify identification of particular fields. However, the method we have reported can be used for improving the analysis of already existing tapes.

Summary

Oscillographic traces of sounds recorded on videotapes can be superimposed easily and synchronously on a duplicate of those tapes. The audio recording remains intact in the duplicate and the oscillotrace allows rather precise analysis of slower movements and the sounds they produce. This system was tested on pre-existing tapes of courtship in the grasshopper *Chortophaga viridifasciata* (De Geer). The method promises to be useful in analysis of tapes used for monitoring behavior and also as a teaching device.

Acknowledgements

We are grateful to Prof. Gershon Berkson for sponsoring our use of the television facilities of the Small Groups Laboratory of the Department of Psychology at the University of Illinois at Chicago Circle. David Mucha helped prepare the photographic figures. Dr. Ruth Willey gave helpful advice during preparation of the manuscript. Technique development and publication were aided by NSF Grant GB-35594 to RBW through the Rocky Mountain Biological Laboratory.

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PSYCHE

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SOCIAL CARRYING BEHAVIOR AND DIVISION OF LABOR DURING NEST MOVING IN ANTS

BY MICHAEL MÖGLICH* AND BERT HÖLLDOBLER
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Social carrying behavior is one of the most remarkable social activities in ant societies. Not only eggs, larvae and pupae, but also adult workers, queens and males are frequently carried by worker ants to various target areas. Although carrying behavior has been observed in many ant species (see review in E. O. Wilson 1971), only a few analytical investigations have dealt with the biological significance of social carrying behavior in ants. Kneitz (1964) reports that in *Formica polyctena* special "storage workers" are passively moved between the summer nest and winter nest. Arnoldi (1932) observed that during the slave raids *Rossomyrmex proformicarum* uses the carrying technique to recruit sister workers to the nest of the slave ants. In *Camponotus herculeanus* social carrying behavior serves as a "social timer" during the nuptial flight activities: males that tend to take off too early or too late during the daily flight periods are carried back into the nest by their worker nestmates (Hölldobler and Maschwitz 1964).

Most frequently, however, carrying behavior is employed during emigration from one nest site to another. If a nest becomes too small and cannot be extended, or if the microclimatic conditions change, the colony searches for a better site. Although the communication signals used by different ant species to organize nest movings vary considerably, adult transport seems to be the basic recruitment technique of most.

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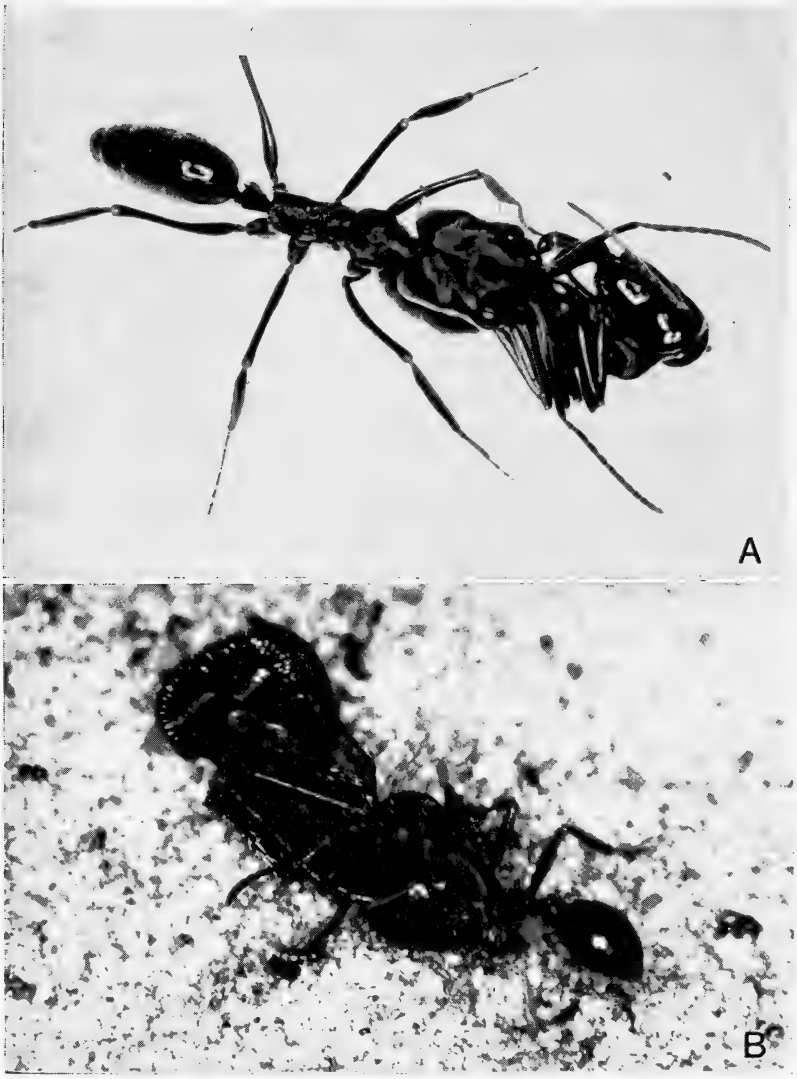

Fig. 1. Primitive adult transport in A) *Odontomachus* (worker carries worker) B) *Pogonomyrmex badius* (worker carries "soldier" caste).

The Specificity and Stereotypy of Carrying Behavior

Escherich (1917) and Arnoldi (1932) pointed out that the behavioral patterns of adult transport in ants are very stereotyped and are often specific for certain taxonomical groups. These assumptions are confirmed by the following brief survey of adult transport behavior in ants.

Myrmeciinae:
In one of the most primitive genera of the myrmecoid complex, the Australian *Myrmecia* Haskins and Haskins 1950 observed adult transport. However, the behavioral patterns are apparently not stereotyped. One worker grasps another at the mandibles or any other part of the body and drags it over the ground.

Dorylinae:
According to Rettenmeyer (1963) workers of the New World army ants (tribe *Ecitonini*) carry other adults like larvae and pupae slung beneath the body and between the legs of the transporting worker.

Ponerinae:
An unstereotyped carrying behavior, similar to that described for *Myrmecia,* was observed by the present authors in *Bothroponera tesserinoda.* It occurs only rarely; nestmates are primarily recruited by the tandem running technique (see Maschwitz, Hölldobler and Möglich, in press). Somewhat more advanced is the adult transport behavior of *Odontomachus.* The transporter ant simply grasps a nestmate on a leg, the petiole or some other part of the body, lifts it up and carries it away. Although there is no general, stereotyped response, the transported individual usually folds its appendages tightly to the body (Fig. 1A). Much more elaborate and stereotyped behavior is displayed by *Rhyditoponera metallica.* When the transporting worker approaches a nestmate head on, it repeatedly grasps the ant at the head and jerks it slightly forward. The movement lasts only 1-2 seconds. The nestmate responds by turning its bodyaxis slightly sideways, whereupon the transporting ant seizes the nestmate with a firm grip. After turning through an angle of approximately 180°, the transportee is lifted and curled over the head of the carrying ant. During transportation the gaster is bent inwards and the appendages folded tightly to the body.

Myrmicinae:
Although Escherich reports that in myrmicine ants the transported ant is grasped at the petiole and carried with the head and legs

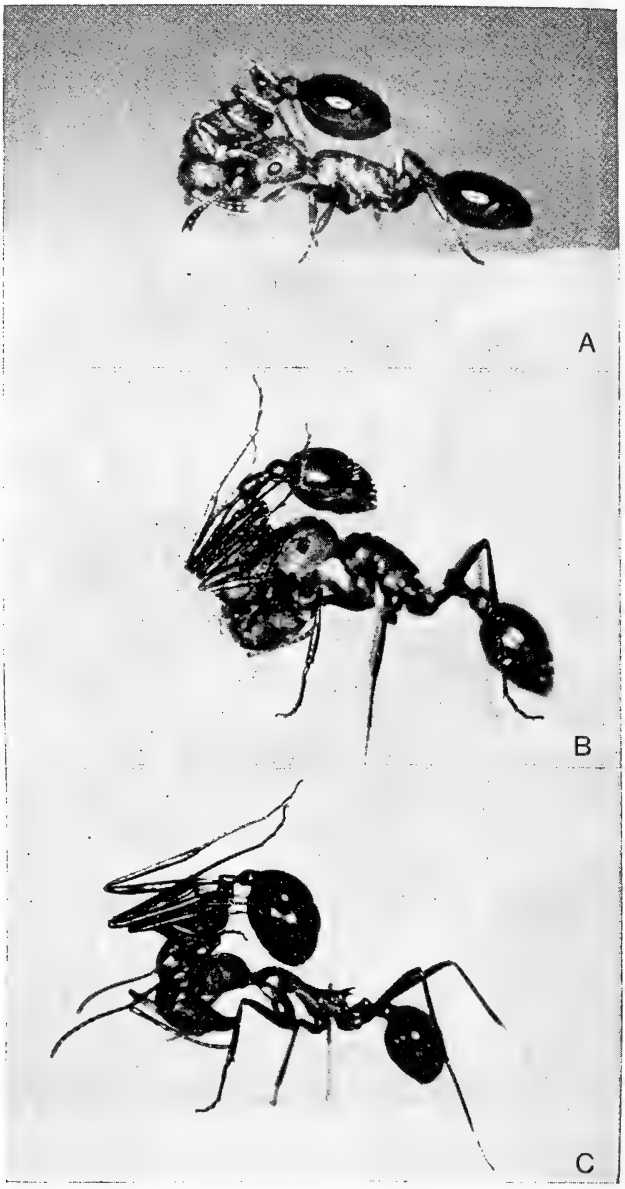

Fig. 2. Adult transport technique in myrmicine ants: A) *Leptothorax nylanderi* (worker carries worker). B) Pogonomyrmex maricopa (worker carries worker). C) *Novomessor cockerelli* (worker carries worker).

pointed forward, in fact this seems to be the exception and has been specifically observed only in *Crematogaster* (see Wilson 1971). Generally, however, the stereotyped adult transport behavior of many myrmicine species, which has been repeatedly described since Escherich's time, resembles that of *Rhyditoponera.* The transportee is either seized at the mandibles or at the "neck" or "cheeks" and curled over the head of the transporting worker (Fig. 2). But there are a few other exceptions: we found, for example, that the harvesting ants *Pogonomyrmex badius, P. rugosus* and *P. barbatus* employ a rather primitive carrying technique. As in *Odontomachus* the transportee is grasped at any part of the body, lifted up and carried away. During transportation the carried individual folds its appendages to the body (Fig. 1B). This primitive transporting behavior is especially remarkable, because in some other *Pogonomyrmex* species, for example *P. maricopa,* we found the typical highly stereotyped adult transport behavior described above for other myrmicine ants (Fig. 2).

Formicinae:

The most uniform and stereotyped social carrying behavior can be observed in the subfamily Formicinae. In several species we have analyzed the behavioral patterns that initiate and guide carrying behavior and found them to be virtually invariant. For the following, more detailed description of this behavior we have chosen *Camponotus sericeus,* a common species on Ceylon. The description is based on single frame analyses of slow motion pictures (Fig. 3).

When a recruiting ant faces a nestmate head on, it conducts a jerking behavior for 2-3 seconds, grasping the nestmate at the mandibles and subsequently pulling it forward. Usually the recruiting ant responds by turning around for 180°. The nestmate is thereby slightly lifted, and this elevation evidently causes it to fold its legs tightly to the body and to roll the gaster inward. In this "pupal" posture it is then carried to the target area.

Identical stereotyped adult transport behavior has been observed in many formicine ants and has been described in particular detail in *Formica rufa* (Zahn 1957), *F. polyctena* (Kneitz 1964, Möglich 1971), *Cataglyphis* (Wehner and Lutz 1969), *Camponotus socius* (Hölldobler 1971) and several other species.

Sex specific carrying postures

Reproductive females are sometimes carried like workers (Fig. 4). But in cases where the size difference is too large, workers merely

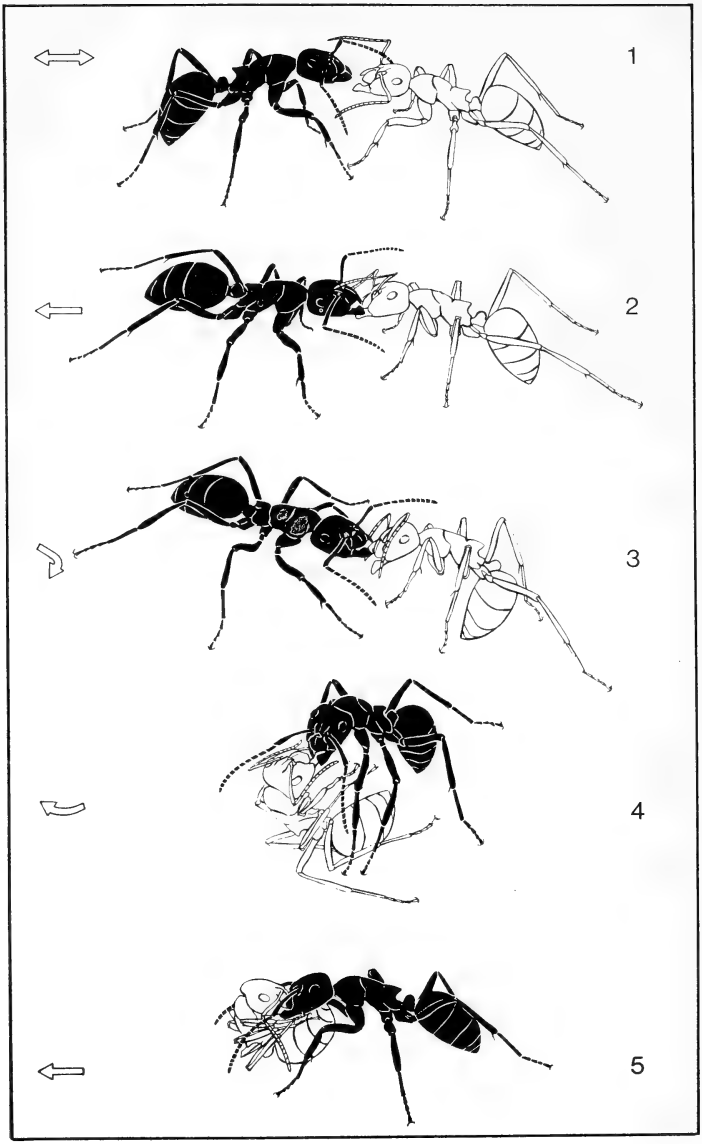

Figure 3

grasp the females at the mandibles and pull them to the target area (Fig. 5). The first behavioral steps that lead to this pulling behavior are usually similar to those which initiate carrying behavior in workers.

The methods by which males are transported are notably different, however. These individuals are sometimes picked up at any part of the body and dragged or carried to the target area. In a few species workers apply specific stereotyped carrying methods for males. In several *Camponotus* species we observed that most of the males are grasped at the "neck" and lifted into an oblique position in which they are carried away (Fig. 6A). During transportation the males remain motionless with the antennae and legs folded to the body. As Fig. 6 B and C shows, there are occasionally exceptions of this carrying technique.

In some other species, as in *Novomessor cockerelli* and *Aphaenogaster floridanus,* workers grasp the males between the thorax and gaster and carry them beneath their body between their legs (Fig. 7).

Division of Labor During Nest Movings

Social carrying behavior in ants can serve many purposes; it is, however, most frequently employed during nest emigrations. Together with the tandem running technique it can be considered to be a rather primitive recruitment method. In both cases, each recruiting ant can only recruit one nestmate at one time. This leads to the question: Do all workers of a colony have the same carrier or tandem-leader potential, or is there instead a group of specialists, who organize nest movings. To investigate this matter we chose two formicine species, one which moves almost exclusively by using the adult transport method (*Formica sanguinea*) and another which primarily employs the tandem running technique (*Camponotus sericeus*).

Nest emigrations can be induced in the laboratory by keeping the

Fig. 3. The behavioral sequences that initiate carrying behavior. 1. The recruiter ant (black) approaches a nestmate (white) and conducts the jerking response for 2-3 seconds. 2. The recruiter grasps the nestmate at the mandibles and pulls it back for about 2-20 cm. 3. When the recruiter turns, it holds the nestmate with a firm grip. The nestmate is thereby slightly lifted. 4. The nestmate folds its legs and antennae tightly to the body and rolls its gaster inward. 5. In this posture it is carried to the target area. The arrows indicate the direction of the movements. These sequences were based on a film analysis. (After Hölldobler, Möglich, Maschwitz 1974; illustrations by Turid Hölldobler).

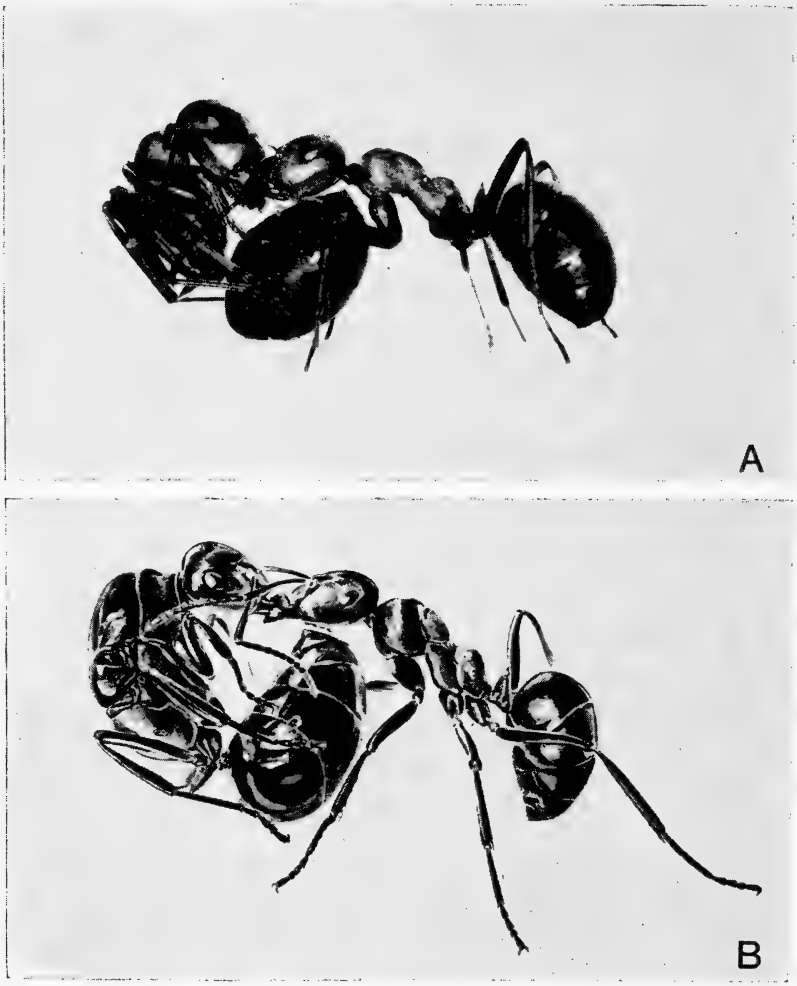

Fig. 4. Adult transport technique in formicine ants: A) *Formica rufa* worker carries a sister worker. B) *Formica rufa* worker carries a queen.

Fig. 5. If the difference of size between workers and queens becomes too large, queens are either pulled or led along a short odor trail to the target area. This is the case in young colonies of *Camponotus pennsylvanicus*.

old nest under less than optimal conditions while at the same time providing a new nest nearby with optimal conditions. Soon a scout discovers the new nest, and after a short inspection returns to the old nest. Usually it runs 2-3 times back and forth between the old and new nest, before beginning to recruit nestmates to the new site. Our intention was to identify and follow all individual workers of an entire colony throughout the experimental procedures. In order to do this we marked the ants individually by applying spots of one or the other of four colors at one or more of four pre-selected positions on the body. In this way we were able to recognize up to 256 workers individually. With each of our test colonies we conducted 20 nest-moving experiments over a period of about 2 months, before the entire colony was killed and each worker subsequently dissected.

During the nest emigrations we recorded the following parameters in particular: 1) How often a worker was carried or led by tandem running, respectively, during all nest movings; 2) How often a worker functioned as a carrier or leader, respectively, during one nest-moving episode and throughout the entire experimental period of 20 movings. 3) We also distinguished between the recruitment intensity and the continuity of the recruitment activity of workers.

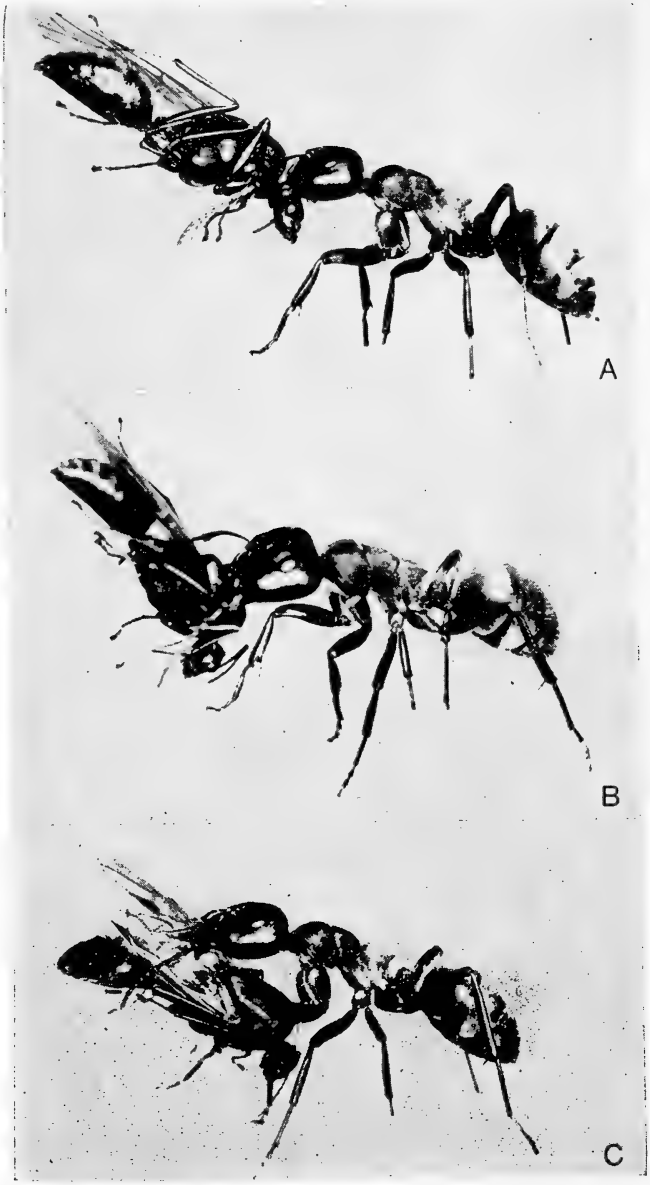

Fig. 6. Male transport in *Camponotus sericeus:* A) Commonly used technique. B) and C) Exceptionally used techniques.

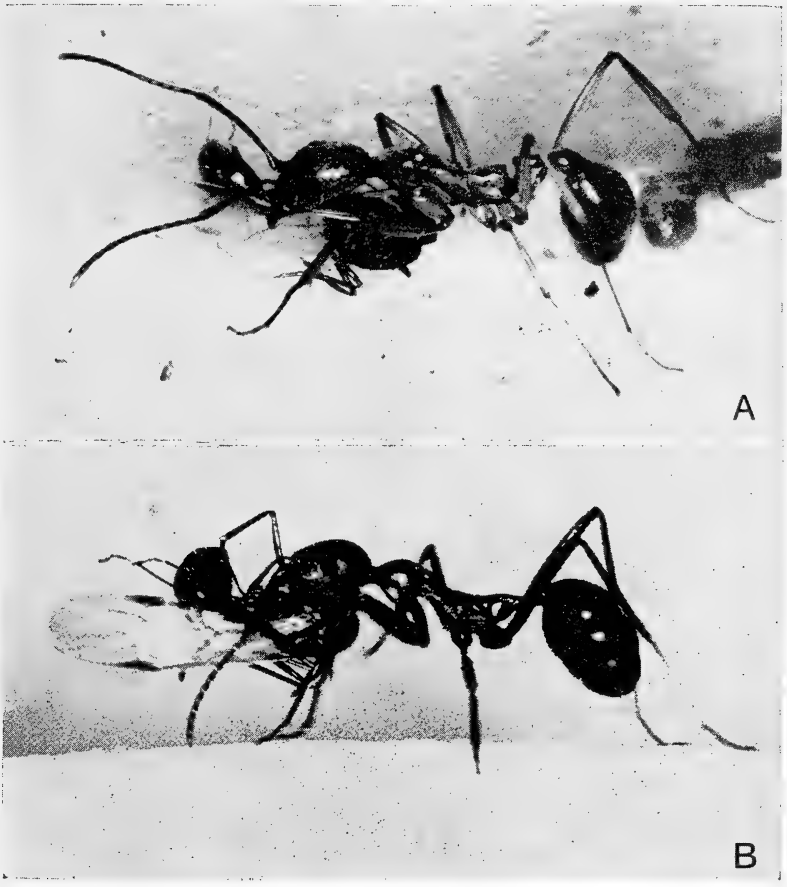

Fig. 7. Male transport in A) *Aphaenogaster floridanus* and B) *Novomessor cockerelli.*

The intensity is defined as the total number of recruitment performances during the entire experimental period, independent how these performances were distributed over the nest movings. The continuity, on the other hand, is defined as the percentage of nest movings during which an individual worker acted at least once as a recruiting ant. 4) In order to rank degrees of specialization of different workers we combined all these parameters in an index which gives us a measure of the relative recruitment activity (RRA) of individual ants: $RRA = \frac{R_a}{R_p} \times C$. R_a is defined as the total number of active recruitment acts performed by the individual ant; R_p is the total number of recruitment episodes during which the ant acted as transportee or tandem follower, respectively, and C is the continuity, as defined above.

The quantitative records gathered for each individual worker during 20 nest movings, are summarized in Fig. 8 and 9. From these sociograms it can be seen that, although both species (*F. sanguinea* and *C. sericeus*) use different recruitment techniques, the social organization of their nest movings is basically similar. The nest emigrations are organized by a pronounced system of division of labor. There is a relatively small group of workers (in our colonies 11% in *F. sanguinea* and 6% in *C. sericeus*) which were active in 80% of all nest moving experiments, and some individuals of this group recruited up to 31 nestmates during a single nest emigration.

This specialized group shows a significantly higher recruitment activity in comparison with all the other workers (X^2-test, $p = 0.01$). The sociograms also reveal that even the mover specialists are sometimes transported themselves. This is especially the case at the beginning of a nest moving, when a single scout ant first recruits workers of the specialists' group. Those recruits subsequently become recruiters themselves. For *F. sanguinea* we recorded at least 7 cases where an ant has been carried to a target area and subsequently returned to the old nest to become a recruiter itself. The same procedure was demonstrated 20 times in *F. polyctena.* From those data we conclude that the carrying act can function as a complete recruitment procedure, by which the recruited ant is not only brought to the target area but also is stimulated to become an active recruiter itself. The same, of course, is true for the tandem running technique as previously documented (Hölldobler, Maschwitz, Möglich 1974).

The degree of specialization of division of labor in different colonies can be demonstrated by ranking the workers according to their

RRA-indices and by plotting the rank positions against the index values (Fig. 10). In the test colonies of both species the curve declines rather steeply indicating that the degree of specialization is high. We were able to prove the crucial role of this small group of specialists simply by removing them from the colony and observing the performance of the workers left behind. Although some regulative replacements by other workers appeared to be possible, the time needed for moving was considerably increased. When we also removed this second mover group, the colony was almost unable to achieve an organized nest emigration, even when their nest conditions became very unfavorable. Workers left the nest and dispersed, but no organized nest emigration took place. From this we conclude that a specialized group of nest movers exists and is important in leading a colony in a relatively short period of time from unfavorable to favorable nest sites.

According to the investigations by Otto (1958) and Kneitz (1964) we should expect that the moving specialists belong to the so called outside workers (Aussendiensttiere) with reduced ovaries. The dissection of all workers of the colonies showed that indeed all movers had reduced ovaries, whereas the ovaries of many of the ants being carried or led were relatively well developed. However, from our invstigations it became also clear that only a small portion of the "Aussendiensttiere" function as mover specialists. If they are removed experimentally, they can be replaced by other workers with reduced ovaries, whereas nestworkers (Innendiensttiere) with well developed ovaries cannot substitute for lost mover specialists.

Summary

Adult transport behavior is a common social activity in many ant species. It is employed most frequently as a recruitment technique during emigration from one nest site to another. As verified in this report, the behavior patterns vary among species and are correlated with phylogenetic groupings.

The social organization of emigration, in particular the division of labor among workers during the process, was analyzed in two species, one of which recruits nestmates by carrying (*Formica sanguinea*) and the other by tandem running (*Camponotus sericeus*). In both cases it was found that only a special group of workers organizes nest emigrations. All these moving specialists have completely reduced ovaries whereas many of the carried or led ants have well developed ovaries.

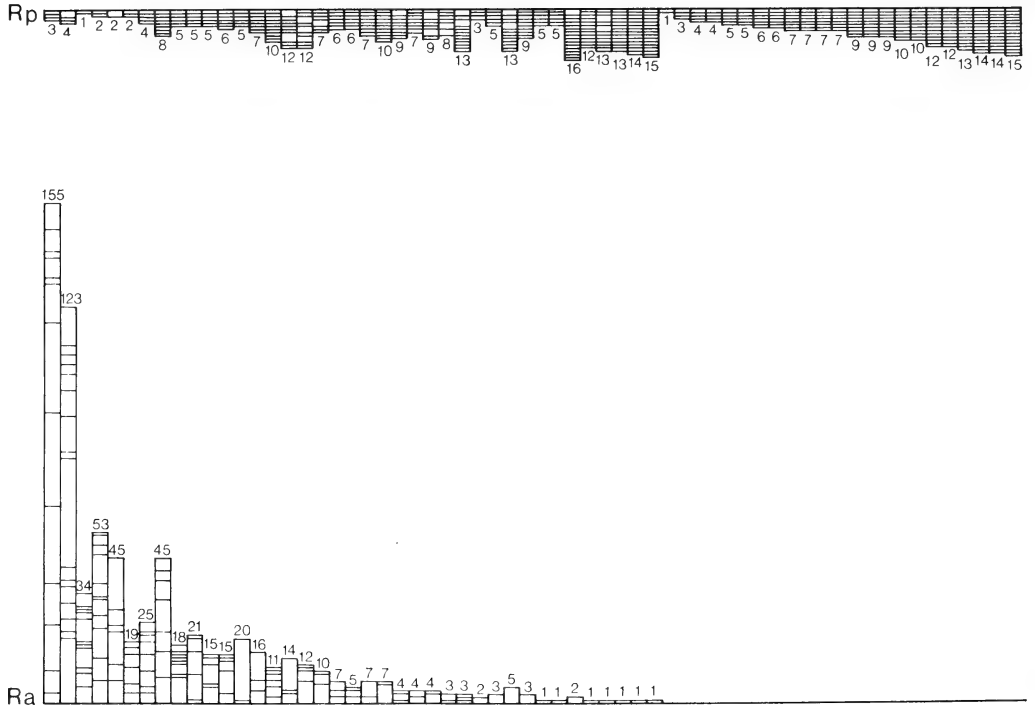

Fig. 8. Sociogram describing the division of labor during nest moving in a *Formica sanguinea* colony. Each pair (Ra and Rp) of columns represents one individual ant. The height of the columns in Ra expresses the total number of acts of recruitment during which the ant carried a nestmate. The number of dashes inside the columns indicates in how many experiments the ant was active as a transporting individual. In Rp the height of the columns expresses the total number of recruitment procedures during which the ant was carried, while the number of dashes indicates in how many nest emigrations this was the case.

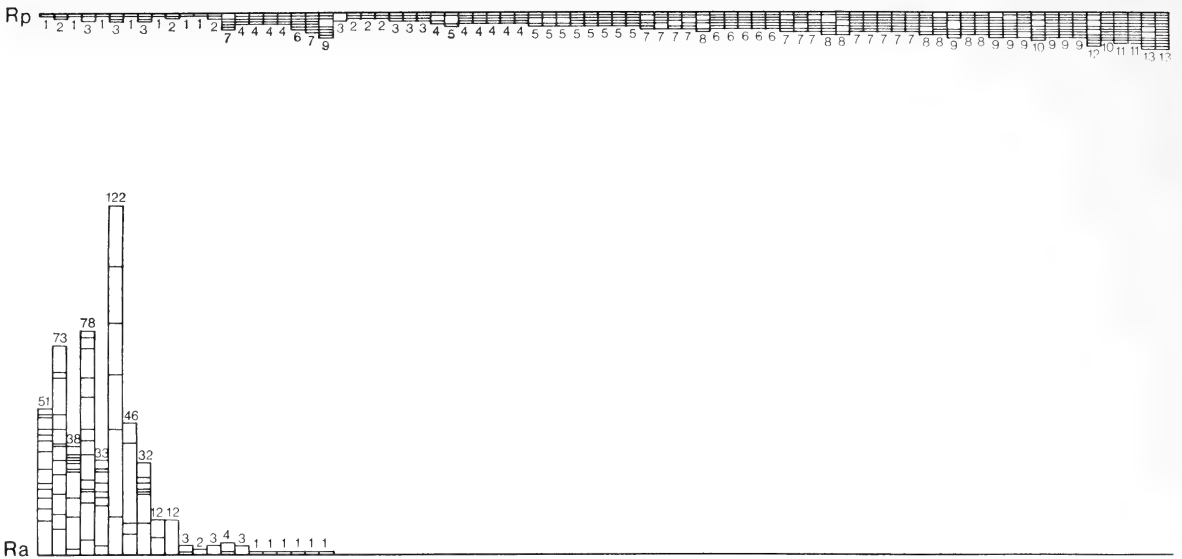

Fig. 9. Sociogram describing the division of labor during nest moving in a *Camponotus sericeus* colony. Each pair (Ra and Rp) of the columns represents one individual ant. The height of the columns in Ra expresses the total number of recruitment acts during which the ant led a nestmate by tandem running to the new nest. The number of dashes inside the columns indicates in how many experiments the ant was active as a recruiting individual. In Rp the height of the columns expresses the total number of recruitment procedures during which the ant was led, while the number of dashes indicates in how many nest emigrations this was the case.

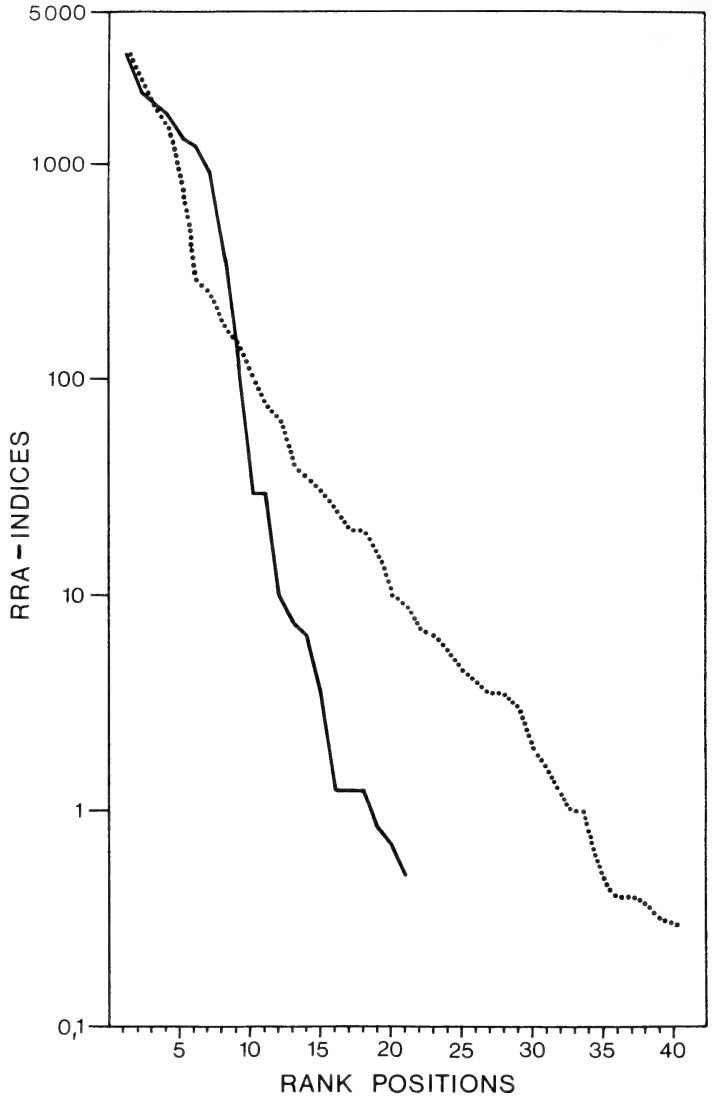

Fig. 10. Individual ants were ranked according to their relative indices. The rank positions (abscissa) are plotted against the index values (ordinate, logarithmic). The steepness of the curve directly represents the degree of specialization of the worker group.

Dotted line: *Camponotus sericeus;* solid line: *Formica sanguinea.*

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TEMPORAL ACTIVITY PATTERNS IN TWO COMPETING ANT SPECIES (HYMENOPTERA: FORMICIDAE)[1]

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Most ant species are known to exhibit some degree of patterning in foraging rate. Interspecific differences in foraging rate can be noted both temporally and, in temperate latitudes, seasonally. Such differences can contribute to an effective partitioning of resources among coexisting species. The following set of observations documents a difference in foraging pattern that may be the significant component of coexistence of the two closely competing species observed. The system will be described, and possible implications of the observations will be discussed.

The species observed were *Dorymyrmex antarcticus* and *Tapinoma antarcticum*[3], both members of the subfamily Dolichoderinae. Observations were made at Fundo Santa Laura, near Til Til, Santiago Province, Chile, during October and November of 1971 and 1972. The site was at 1,000 m elevation on the east-facing slope of the low coastal cordillera. Vegetation was mixed shrubs and annuals forming the community known as matorral, which is characteristic of the Mediterranean climate zone of central Chile.

On visits to the site in 1971 I noted that the two species compete strongly for baits. A bait of honey on a small wad of cotton would attract *Dorymyrmex antarcticus* workers when it was placed on the ground in the early morning. These workers recruited a small number of nestmates, and activity would continue until midmorning when the first few workers of *Tapinoma antarcticum* appeared. These workers, once they located the bait, would quickly recruit many of their nestmates, and the many small *T. antarcticum* workers aggressively repelled the fewer, larger, less aggressive workers of

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[3]Generic placement of this species in *Tapinoma* is almost certainly incorrect. Ecologically, the species is similar to *Iridomyrmex pruinosum* of the southwestern U. S.

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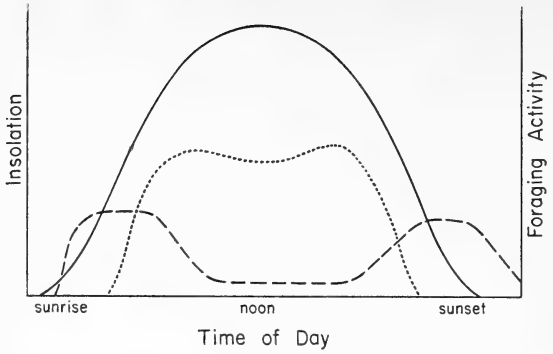

Figure 1. Activity patterns of the two ant species as observed in 1971. Solid line = solar intensity; dotted line = *Tapinoma antarcticum* foraging activity; dashed line = *Dorymyrmex antarcticus* foraging activity.

D. antarcticus. The *Tapinoma* workers continued on the bait throughout the midday, whereas the *Dorymyrmex* workers retreated to their nests, apparently to avoid the high midday temperatures. Late in the afternoon, as temperatures dropped, the *Tapinoma* workers would retreat to their nest leaving the bait to be reoccupied by *Dorymyrmex* workers. Activity at the bait seemed in general to parallel the apparent activity patterns of the species, which I illustrated as in Figure 1. The apparent tolerance of cooler temperatures granted an exclusive period of foraging activity to *D. antarcticus;* aggressive dominance yielded foraging success for *T. antarcticum* during the period when both species were active simultaneously.

In 1972 I documented these patterns quantitatively. Closely adjacent nests of each species were chosen, and counts of workers passing the nest entrance during a two-minute period each half-hour were tallied with hand counters. Soil surface temperatures were monitored with a bulb-type thermometer placed touching the soil near the nests. Solar intensity values were taken from a pyroheliometer (Belfort Inst. Co.) stationed 150 m from the study nests. The pattern documented for one nest of each species on 4 October is illustrated in Figure 2a.

On the following day I returned to the same nests to document the early morning activity missed the preceding day. The patterns for 5 October are shown in Figure 2b. The day was cloudy and cool, and differences in foraging activities of the ants are of interest. The *D. antarcticus* continued active all day. The *T. antarcticum* workers emerged later and were out in fewer numbers than on the

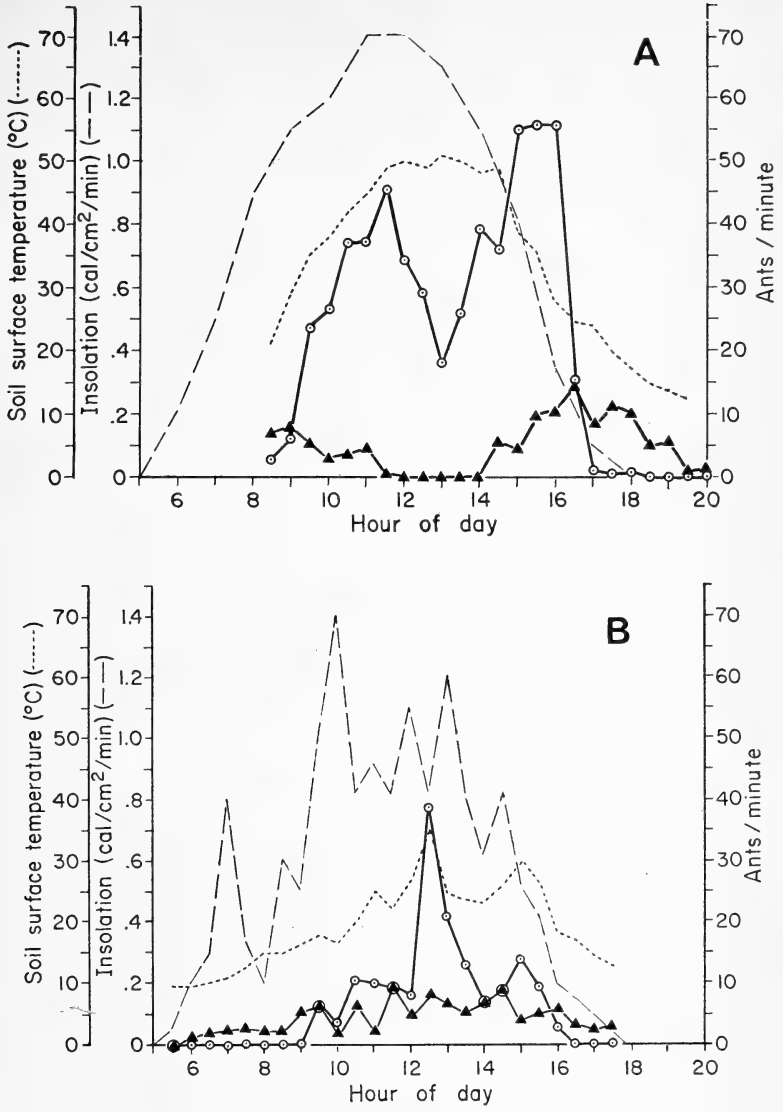

Figure 2. Activity patterns of the two ant species as documented in 1972; A = 4 October, B = 5 October. Triangles = *Dorymyrmex antarcticus;* circles = *Tapinoma antarcticum* (both in ants per minute passing nest opening); dotted line = soil surface temperature (°C); dashed line = solar intensity (cal/cm²/min).

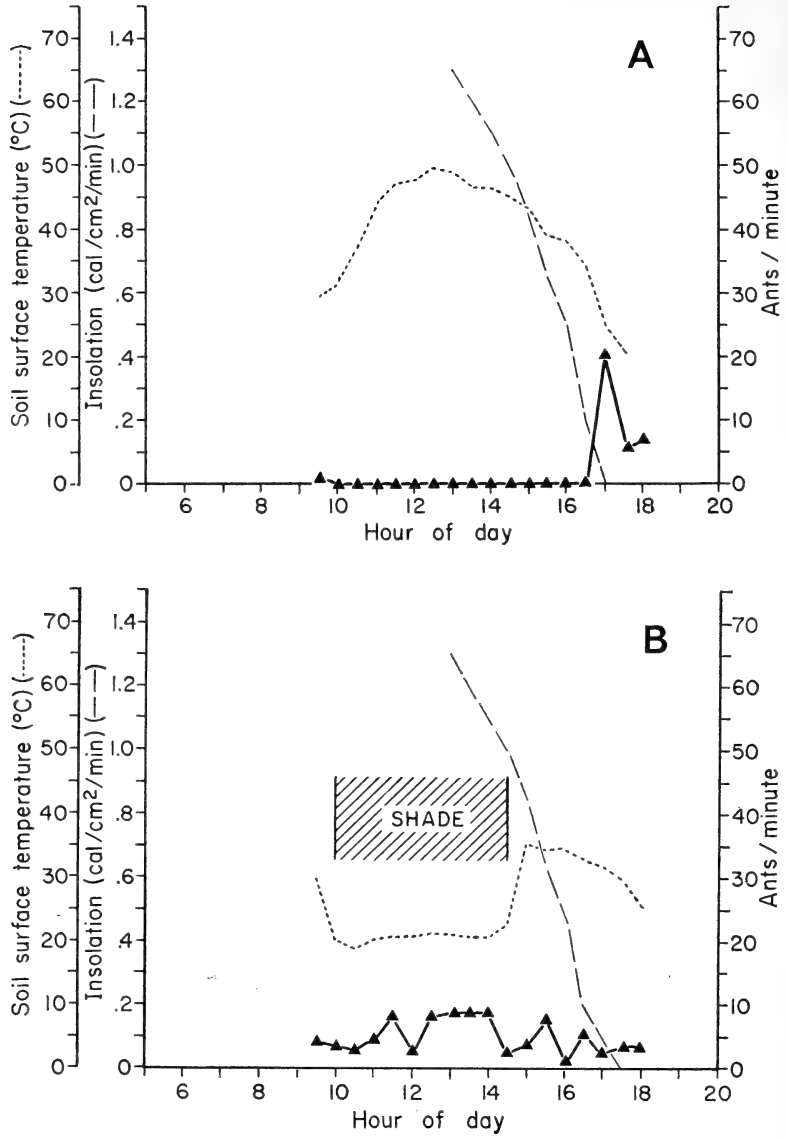

Figure 3. Activity patterns of *Dorymyrmex antarcticus* on 19 October with and without experimental shading of nests; A = an unshaded nest, B = a shaded nest.

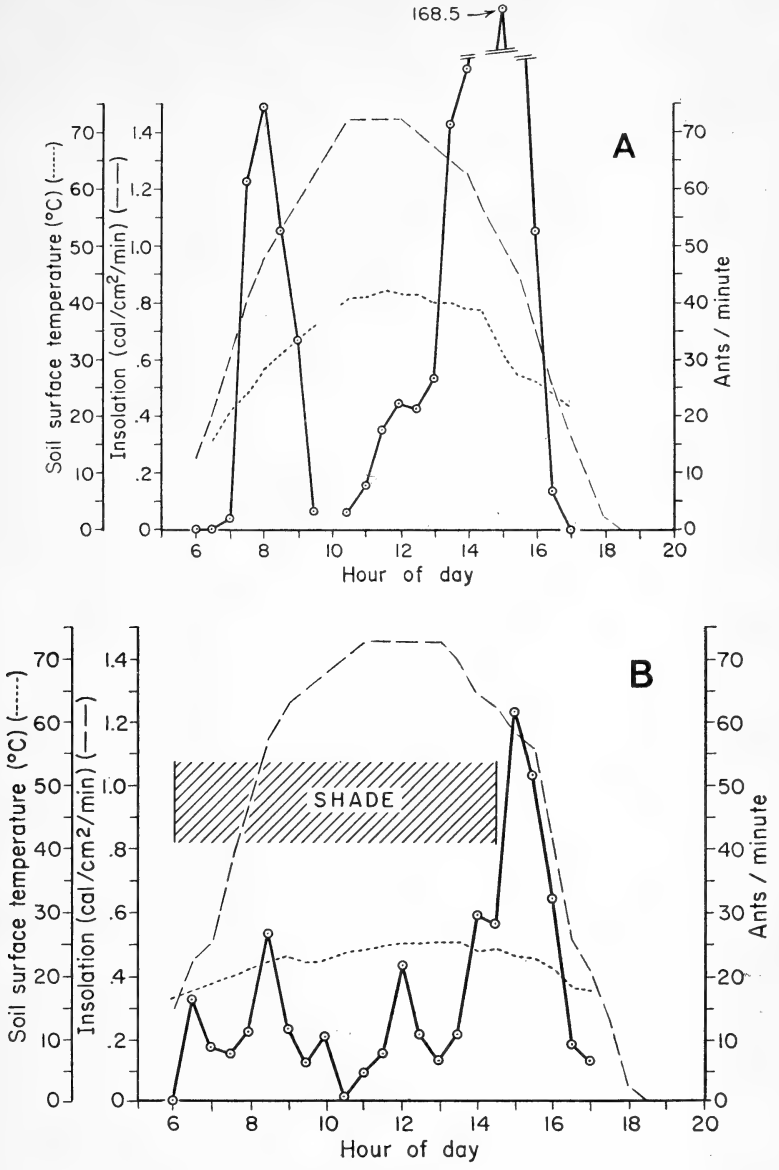

Figure 4. Activity patterns of *Tapinoma antarcticum* with and without experimental shading of the nest; A = 1 November (unshaded), B = the same nest on 2 November (shaded).

preceding day, with activity peaks corresponding to peaks of soil warmth. It seemed that foraging rates of the species were mediated by soil surface temperatures.

On 19 October I tested this hypothesis by using a Thermos Brand Space Blanket (a highly reflective material) to shade a nest of *D. antarcticus* on a hot, sunny day. Figures 3a and 3b show activity patterns at two neighboring nests of similar size. Workers of the unshaded nest illustrate the expected pattern, but workers from the shaded nest continued foraging throughout the day. Figures 4a and 4b show a similar test with *T. antarcticum*. Figure 4a illustrates activity of a single colony on 1 November; Figure 4b is the same nest, shaded, on 2 November. The shading yielded a marked reduction in foraging rate. The late afternoon peak is of workers carrying larvae and pupae and emigrating to a new nest site under unshaded stones about 1 m from the shaded site.

Discussion

The two species studied have similar food and foraging site preferences. The observed differences in temporal foraging pattern are hypothesized to contribute significantly to the species' coexistence. Soil surface temperature seems to be the proximate factor by which the foragers regulate their activity. Endogenous activity rhythms, often keyed to environmental factors, are known for many species. This study illustrates how variation in environmental factors can yield alteration of the activity rhythms.

During the course of a year at this temperate latitude (33° S) it seems probable that *Dorymyrmex antarcticus* would have more foraging hours available to it, especially during spring, fall, and winter days, than would *Tapinoma antarcticum*. Perhaps the aggressive dominance of *Tapinoma* is a necessary requisite for survival in competition with other species. The rapid recruitment of a large number of rather small workers in *Tapinoma* may illustrate components of a foraging strategy that must yield successful foraging returns during activity periods that are more limited than those of a coexisting competitor.

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RELATIONSHIP OF LARVAL FOOD-PLANTS AND VOLTINISM PATTERNS IN TEMPERATE BUTTERFLIES*

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An interesting aspect of phenology is the number of broods that a species produces in the growing season. Even among a fairly uniform group like the butterflies within a restricted geographical area, voltinism patterns of the different species may vary considerably. Explanations of possible causes of, and ecological implications of these patterns have apparently seldom been attempted.

It might be expected that voltinism patterns are often genetically determined and are regulated by some environmental clue (cf. Wigglesworth, 1967), but knowing the proximate reason does not reveal the ultimate causes that brought the voltinism patterns under such control. Obviously, the presence of a food source for the larvae (and, although less well studied, for the adults as well) will have a major influence on these patterns. The exclusive use of the vernal herb *Dentaria* by larvae of the West Virginia white, *Pieris virginiensis,* precludes any more than one brood per season. As an adaptation to feeding on this ephemeral food-plant, the larvae upon entering the pupal stage undergo obligate diapause, even though the genetic mechanism for multivoltinism exists in this species (Shapiro, 1971).

A more subtle explanation of voltinism patterns may emerge from examining larval growth rates on different plants (e.g. Dowdeswell & Willcox, 1961; Hovanitz & Chang, 1962; Sharifi & Zarea, 1970). Nutritional (including water) differences (Soo Hoo & Fraenkel, 1966; Waldbauer, 1968; Feeny, 1970; J. M. Scriber and P. P. Feeny, ms. in prep.; Slansky, 1974) and differences in secondary chemical content (Gupta & Thorsteinson, 1960; Nayar & Thorsteinson, 1963; Feeny, 1970) of different plant species and of the same plant species at different stages of growth in large part determine the growth rates of larvae feeding on the plants, and thus perhaps for

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some species, voltinism patterns as well. The purpose for this work is to examine the hypothesis that, of the butterflies in particular climatically similar areas, those which have larval food-plants that are apparently nutritionally unsuitable for much of the growing season will exhibit in general fewer broods per season than those butterflies which have larval food-plants that are apparently nutritionally adequate throughout the season.

Methods

In order to examine the hypothesis the number of broods produced per year by, and the larval food-plants of, eighty-six species of butterflies were tabulated for three transition zone areas in eastern and mid-western United States (Forbes, 1906; Saunders, 1932; Ebner, 1970). Additional food-plant records were obtained from Ehrlich and Ehrlich (1961) and Shapiro (1966). The voltinism patterns of selected species of these butterflies were then related to changes in the nutritional suitability of their larval food-plants.

Results and Discussion

That differences in larval growth rates are reflected in the voltinism patterns of butterflies is seen in the following example. Under similar temperature and humidity conditions the duration of the larval stage of the imported cabbageworm, *Pieris rapae,* is about 15 to 20 days on some of its food-plants (Slansky, 1974), while that of the Eastern tiger swallowtail, *Papilio glaucus,* is about 35 to 45 days on some of its food-plants (J. M. Scriber, unpublished data). As a consequence, *P. rapae* generally exhibits one brood more than *P. glaucus* in the areas where they occur together (Table 1).*

Further support for the hypothesis is found when the voltinism patterns of selected butterfly species are examined in relation to seasonal changes in the nutritional suitability of larval food-plants. For example, species whose larvae feed on oaks (*Quercus*), such as the hairstreaks *Satyrium edwardsii, S. liparops,* and *S. calanus,* and the skippers *Erynnis brizo, E. horatius,* and *E. juvenalis,* usually have

*Although *P. glaucus* is generally considered to have two broods in the areas surveyed in this study, it may be that there is only one 'true' brood. It appears that a high percentage of the pupae from the previous season emerge in the early summer, constituting the 'true' first brood, and that the remaining pupae emerge later in the summer, constituting an 'apparent' second brood (i.e., not the progeny of the first brood of that season) (Scudder, 1889; R. Lederhouse and J. M. Scriber, unpublished data).

TABLE 1. Number of broods, larval food-plants, and hibernating stages for several butterflies in three transition zone areas. Data from Forbes (1906), New England (A); Saunders (1932), Allegany State Park, N.Y. (B); and Ebner (1970), Wisconsin (C). E = egg; L = larva; P = pupa; A = adult.

Species	Number of Broods A	B	C	Larval food-plants	Hibernating Stage
HESPERIIDAE					
Amblyscirtes samoset	1	–	1	Gramineae	?
A. vialis	2	–	1	*Andropogon*	P
Euphyes dion	–	–	1?	*Scirpus, Carex?*	?
E. conspicus	–	–	1	*Carex*	?
Poanes massasoit	2	–	1	*Carex*	?
P. hobomok	1	1	1	*Poa, Panicum*	L,P
P. viator	–	–	1	*Zizania, Phragmites?*	?
Wallengrenia otho	–	1	1	*Panicum, Digitaria*	L
Polites coras	1	–	2	Gramineae	?
P. themistocles	–	–	1–2	*Panicum*	?
P. mystic	2	2?	1	*Poa*	L
Hesperia metea	1	–	1	*Andropogon*	?
H. sassacus	1	1	1	*Panicum*	?
H. leonardus	1	–	1	*Panicum, Erogrotis*	L
Ancyloxipa numitor	3	3	2–3	*Poa*	L,P
Pholisora catullus	2	–	1	*Chenopodium, Amaranthus, Ambrosia, Marrubium*	L
Pyrgus communis	–	3	2	*Althaca, Malva*	L,P
Erynnis icelus	1	1	1	*Populus, Betula*	L
E. brizo	1	–	1	*Quercus, Castanea*	L
E. lucilius	3	–	2	*Aquilejia*	L
E. horatius	2	–	–	*Quercus*	?
E. juvenalis	2	–	1	*Quercus*	L
Thorybes bathyllus	1	–	1	Leguminosae	P
T. pylades	2	2?	1	*Lespedeza, Trifolium, Medicago*	P
Epargyreus clarus	1	2	1-2	*Robinia, Wistaria*	P
PAPILIONIDAE					
Battus philenor	2	2	–	*Aristolochia*	P,A
Papilio polyxenes	2	2	2	Umbelliferae	P
P. glaucus	2	2	1–2	*Fraxinus, Prunus, Betula, Populus,* others	P
P. troilus	2	2	–	*Lindera, Sassafras, Persea*	P

Species	Number of Broods A	B	C	Larval food-plants	Hibernating Stage
PIERIDAE					
Pieris protodice	3	–	3	Cruciferae	P
P. napi	3	–	3	Cruciferae	P
P. virginiensis	–	–	1	*Dentaria*	P
P. rapae	3	3	3	Cruciferae	P
Colias eurytheme	3	3	3	*Medicago, Trifolium*	P
C. philodice	4?	3	3	*Trifolium*	L?
C. interior	1	–	1	*Vaccinium*	?
Anthocaris midea	1	–	–	Cruciferae, esp. buds, flowers, seeds	P
LYCAENIDAE					
Harkenclenus titus	1	1	1	*Prunus*	E
Satyrium liparops	1	1	1	*Quercus, Salix, Rubus, Malus, Prunus, Vaccinium,* others	E
S. calanus	1	1	1	*Quercus, Carya, Castanea*	E,L
S. edwardsii	1	–	1	*Quercus*	E,L
S. acadica	1	1	1	*Salix*	E
Callophrys irus	1	–	–	*Babtisia, Crotalaria, Lupinus,* esp. flowers, fruit	P
C. henrici	1	–	1	*Vaccinium, Prunus, Cercis,* bores into flowers	P
C. augustinus	1	–	1	*Vaccinium, Kalmia, Arbutus, Arctostaphylus, Ceanothus,* esp. flowers and berries	P
C. niphon	1	–	1	*Pinus*	P
C. gryneus	1–2	–	2	*Juniperus*	P
Strymon melinus	2	–	2	*Polygonum, Phaseolus, Malva, Hypericum, Humulus,* others, bores into bud, fruit	?
Lycaena thoe	2	2	3	*Rumex, Polygonum*	E
L. epixanthe	1	–	1	*Vaccinium*	E
L. phlaeas	3	2	3	*Rumex*	P,L?
Everes comyntas	3	3	3–4	Leguminosae, foliage, buds, flowers	L
Celastrina argiolus	2	2	2	*Cornus, Rhus, Vaccinium, Cimicifuga, Ceanothus,* others	P
NYMPHALIDAE					
Asterocampa celtis	2	–	2	*Celtis*	L
A. clyton	2?	–	2	*Celtis*	L
Limenitis arthemis	1–2	1–2	2	*Salix, Betula, Populus, Tilia*	L

Species	Number of Broods A	B	C	Larval food-plants	Hibernating Stage
L. astyanax	1–2	2?	2	*Prunus, Malus, Pyrus, Crataegus, Salix, Populus*	L
L. archippus	2	2	2	*Salix, Populus, Prunus, Malus*	L
Vanessa atalanta	2	2	2	Urticaceae	P,A
V. virginiensis	2	2	2	*Artemisia, Gnaphalium, Antennaria,* others	P,A
V. cardui	2	2	2	*Cirsium, Carduus*	A,P?
Junonia coenia	2	–	–	*Plantago, Gerardia, Sedum, Antirrhinum*	A?
Nymphalis vau-album	2?	2?	2?	*Betula, Salix, Populus*	A
N. milberti	3	2	3	*Urtica*	A
N. antiopa	2	2	2	*Ulmus, Celtis, Salix, Populus*	A
Polygonia interrogationis	2	2	2	Ulmaceae, Urticaceae	A
P. comma	2	2	2	Ulmaceae, Urticaceae	A
P. faunus	1	1	1	*Betula, Salix, Alnus, Ribes*	A
P. progne	2	2	2	*Ribes*	A
Chlosyne nycteis	2	1	1	*Helianthus, Actinomeris, Aster*	L
C. harrisii	1	1	1	*Aster*	L
Phyciodes tharos	2	2	2	*Aster*	L
P. batesii	2?	1	1	*Aster*	L?
Euphydryas phaeton	1	1	1	*Chelone*	L
Bolaria selene	3	3	2–3	*Viola*	L
B. toddi	3	3	2	*Viola*	L
Speyeria idalia	1	1	1	*Viola*	L
S. atlantis	1	1	1	*Viola*	L
S. cybele	1	1	1	*Viola*	L
S. aphrodite	1	1	1	*Viola*	L
DANAIDAE					
Danaus plexippus	2	2	2	*Asclepias*	Migratory
SATYRIDAE					
Lethe portlandia	1	1	1	Gramineae, Cyperaceae?	L
L. eurydice	1	1	1	Gramineae, Cyperaceae?	L
Euptychia cymela	1	1	1	Gramineae	L
Cercyonis pegala	1	1	1	Gramineae esp. *Tridens*	L
Oeneis jutta	1	–	1	Gramineae, Cyperaceae	L

one, or at most two, broods, and most hibernate in the larval and/or egg stage (Table 1). This may be due to the presence in the oak leaves of tannins that restrict protein utilization and hinder larval development, in many cases limiting consumption of the foliage to spring and early summer when the protein content is highest and the tannin content lowest (Feeny, 1970).

In addition, the leaves of many species of shrubs and trees contain substantially lower percentages of water than the leaves of many annual and perennial herbs (Way, 1853; Fagin & Watkins, 1932; Soo Hoo & Fraenkel, 1966; Slansky, 1974; J. M. Scriber, unpublished data). Since the percentage of water in most lepidopterous larvae appears to be about 80 to 90% (Evans, 1939a; 1939b; Wigglesworth, 1967; Slansky, 1974; J. M. Scriber, unpublished data), the growth of larvae feeding on plants with a percentage of water lower than their own tissue may be limited by the availability of water so that they exhibit slower growth rates in comparison to larvae feeding on plants that have a percentage of water equal to or greater than that of the larvae (Southwood, 1972; J. M. Scriber & P. P. Feeny, ms. in prep.). The fact that a number of tree and shrub feeders exhibit but one or two broods (Table 1) supports this contention. Along these lines Feeny (1974) has suggested that plant species that are abundant and/or persistent have apparently evolved "quantitative" defenses (low nutrient contents, tough leaves, high contents of unspecific chemicals like tannins) that act as significant ecological barriers to phytophagous insects, in contrast to plant species that are rare and/or ephemeral that have apparently evolved "qualitative" defenses (specific secondary chemicals) that act as only slight ecological barriers to adapted insects although having considerable impact as evolutionary barriers to non-adapted insects.

The majority of grass- and sedge-feeders (all Satyridae and several Hesperiidae), with characteristically sluggish larvae (Scudder, 1889), exhibit but one brood (Table 1). In view of the low moisture and high fiber content of many grasses (Way, 1853; Watson, 1951), it is not surprising that larval development might be slow on such plants. The hibernation of many of these satyrids and hesperiids as early instar larvae (Table 1) may be an adaptation for the avoidance of nutritionally poor, mature grass plants and for the maximum utilization of the spring flush of succulent growth when moisture and nitrogen levels are high and fiber content low (Watson, 1951).

Thus, the voltinism patterns of several butterfly species are given an ecological meaning, and the hibernation of many butterfly species as eggs, larvae, and perhaps fertile adults (Scudder, 1889), when

viewed as a means of utilizing tender, nutritious plant tissue in the spring, is seen as an adaptive strategy (c.f. Morse, 1971; Schoener, 1971). Of course, it is not suggested that the nutritional quality of the larval food-plant is of sole importance in determining voltinism patterns. For example, larvae of both the Tawny crescent, *Phyciodes batesii,* and the Pearl crescent, *P. tharos,* feed on *Aster;* the former exhibits one brood and the latter two or three (Table 1). Larvae of two *Bolaria* species and of four *Speyeria* species all feed on *Viola;* the former exhibit two to three broods, the latter one brood (Table 1). There may be differences in the nutritional quality of different species of plants within these genera, but other factors appear to be causing these differences in voltinism patterns. The Least skipper, *Ancyloxipa numitor,* larvae of which feed on what might be characterized as 'nutritionally poor' grass plants, exhibits two or three broods while the Eastern black swallowtail, *Papilio polyxenes,* larvae of which feed on what might be characterized as 'nutritionally adequate' plants in the Umbelliferae, exhibits but two broods (Table 1).

Obviously, the interaction of several other factors (e.g. larval size, larval mortality rates, and the presence of adult nectar sources) with the nutritive and secondary chemical contents of the larval food-plants influences the voltinism patterns. For example, the slow growth rates of larvae of *P. glaucus* may only be 'permitted' because the combination of the patchy distribution and warning coloration of the larvae may reduce mortality losses from predators and parasitoids (J. M. Scriber, personal comm.). On the other hand, the rapid growth rates of larvae of *P. rapae* may be a 'necessity' because of the nature of its food-plants (i.e., mostly early successional species) and because of the high mortality losses of the larvae to predators, parasitoids, and disease (Richards, 1940; Pimentel, 1961; Dempster, 1969; Parker, 1970). The more rapid growth rates of lepidopterous larvae from 'geographical races' occurring in regions with short growing seasons in comparison to those of larvae from regions with longer growing seasons (Goldschmidt, 1940) provides another example of the ecological importance of differences in larval growth rates.

Such considerations of the interrelationship of life history phenomena and population dynamics (e.g. Cole, 1954; Murdock, 1966; Istock, 1967; Gadgil & Bossert, 1970; Morse, 1971; Schoener, 1971; Willson, 1971) raise a number of ecologically relevant and as yet insufficiently answered questions, such as:

1) What are the advantages of monophagous and polyphagous larval feeding habits (c.f. Brues, 1920; 1924; Buxton, 1923; Dethier, 1954; Brower, 1958; Schoener & Janzen, 1968; Levins & MacArthur, 1969)?

2) Why do some butterflies exhibit a long-lived adult stage (e.g. almost a full year in the Tortoise shell, *Nymphalis vau-album*) (c.f. Murdoch, 1966; Howe, 1967; Gadgil & Bossert, 1970)?

3) What selective forces cause the complex voltinism pattern exhibited by a number of butterfly species in which part of a brood becomes dormant while the remainder continues normal development (Scudder, 1889; Oliver, 1972)? Perhaps this may allow these species to exploit marginally favorable periods while maintaining a reserve population for the usually favorable season and/or may aid in reducing losses to temporally restricted predators and parasitoids (c.f. Baltensweiler, 1968; Waloff, 1968).

4) Why do some butterflies exhibit multivoltinism? Perhaps this is a means of building up large populations to withstand high mortality losses in the summer, especially because of biological causes, and in the winter, especially because of physical causes, such as is seen in several pierid butterflies that start out with low population levels in the spring and become more abundant as the summer progresses (Scudder, 1889).

Detailed ecological studies of a taxonomically and geographically well-known group like the butterflies will help to answer such questions and will aid in making meaningful predictions about such important phenomena as the population buildup of a potential or actual pest species.

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VARIATIONS IN CLEANING BETWEEN THE SEXES OF *SINELLA COECA* (COLLEMBOLA: ENTOMOBRYIDAE)*

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With the widespread and frequent occurrence of pheromones among insects, it is easy to appreciate the significance of cleaning and grooming behaviors. However these behaviors are as yet poorly known. Among springtails two papers by Simon (1961, 1963) present the most thorough reports. These describe the types of cleaning in representatives of several families, noting the widespread, though infrequent, use of cleaning droplets released from the mouth.

My work examines *Sinella coeca* (Schott) (Family Entomobryidae) for behavioral differences between the sexes. In particular, I have determined the frequency of cleaning and the duration of bouts of cleaning behavior. The initial expectation is that the sexes will spend about equal time cleaning. However, since males are more active, moving about most of the time, their bouts of cleaning are probably shorter. To compensate, I expected males to have more frequent cleaning sessions. An experiment was carried out to test these expectations.

Methods

Sinella coeca was reared in mass culture as described previously for *Sinella curviseta* (Waldorf, 1971). Cultures were maintained at room temperature (23° ± 1°C) and supplied commercial yeast as food. Males and females were isolated in individual glass vials with plastic caps. The vials, measuring 18.1 mm in inner diameter, contained a moist plaster of paris-charcoal substrate (to maintain high humidity) and food. After 24-26 hours of isolation, each animal was observed for five minutes, and the number of bouts of cleaning and the total time (out of 5 minutes) engaged in cleaning recorded. This procedure was followed for 50 males and 50 females. To prevent bias the vials were mixed so that during the observation periods the sex of test animals was usually unknown.

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Table 1. Characteristics of male and female bouts of cleaning behavior.

	Number of bouts/animal			Length of bouts (in sec)		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD
Males	1.88	50	1.33	29.4	94	38.6
Females	1.38	50	1.23	23.8	69	29.5

Results

The data in Table 1 present the overall characteristics of males and females. Comparison of the lengths of bouts using a t-test shows that these are not significantly different ($t = 1.049$). However the number of bouts is significantly larger in males than in females ($t = 1.949$; $.05 > P > .01$). Rather than the expected differences, it appears that male sessions of cleaning are of equal length and more frequent than those of females.

At times of observations some individuals were pharate, some vials contained exuviae and others eggs. These allowed the animals to be subdivided into groups corresponding approximately to position in instar. Among the males only two ecdysed within the 24 hour isolation period, a sample too small to be meaningful. However among the females, the categories were sufficiently large to permit evaluation.

Table 2 gives the data for females of different types. Of the four pharate females, none exhibited any cleaning behavior. Comparison of recently ecdysed females and females with eggs to remaining females revealed no significant differences in bout length. In contrast, comparisons of cleaning frequency among these females showed that females with eggs clean significantly more often ($t = 2.488$; 25df; P .01) than other females.

Discussion

As Simon (1961) has noted, the antennae, the location of important sensory receptors, are cleaned most often. There is possibly a positive correlation between frequency of cleaning and the required sensitivity of receptors. In pharate females the old receptors have presumably lost their nervous connections, so that there is no adaptive advantage in cleaning them. In contrast, females that have recently deposited eggs are sensitive to the required stalked spermatophores on the substrate. If this species has alternate reproductive and non-

Table 2. Characteristics of cleaning bouts by females of various types.

	Number of bouts/animal			Length of bouts (in sec)		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD
Pharate females	0	4	0	—	—	—
Recently ecdysed females	1.63	19	1.34	22.4	31	29.0
Females with eggs	2.1	9	1.05	20.8	19	28.9
Other females	1.05	18	1.00	29.1	19	31.7

reproductive instars with oviposition confined to early in the reproductive instar as *Sinella curviseta* (Waldorf, 1971), newly ecdysed females are possibly a mixture of two types: sensitive ones early in the reproductive interval and indifferent, or less sensitive ones, early in the nonreproductive instar. Although the distribution of numbers of cleaning bouts per female is not bimodal, the mean of this category is 1.63, approximately the average (1.57) of the sensitive group with eggs and the remaining females. Note also that the variance of the number of bouts of recently ecdysed females is 1.796 and that of females with eggs and remaining females are 1.102 and .998 respectively.

Considering males, Mayer (1957) has reported that males of *Sminthurides aquaticus* Bourlet clean more frequently when clasping the antennae of females than when alone. This is consistent with the hypothesis that these males are highly sensitive to olfactory stimuli.

The data indicate that males engage in more total cleaning than females. My recent studies of *Sinella curviseta* (Waldorf, in manuscript) demonstrate that females of this species produce a sex pheromone. This stimulates spermatophore deposition by males in the reproductive instar. Of the males in the present study 48 of 50 were in the reproductive instar at observation time. By frequent cleaning, these maintain their sensitivity to olfactory stimuli including possible pheromones.

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Centennial of Entomology. Cornell University has announced a Centennial of Entomology, celebrating John Henry Comstock's graduation and the founding of studies in entomology at the University. A symposium on *Insects, Science and Society* will be held on October 14 and 15, 1974. The speakers at the symposium will be as follows:

Howard E. Evans, Colorado State University: *The Comstock Heritage.*

John J. McKelvey, Jr., The Rockefeller Foundation: *Insects and Human Welfare.*

Edward O. Wilson, Harvard University: *Insect and Human Societies.*

John S. Kennedy, Imperial College Field Station, Ascot, England: *Insect Dispersal.*

Richard D. Alexander, University of Michigan: *Insect Communication — Acoustical.*

Wendell L. Roelofs, New York State Agricultural Experiment Station, Geneva: *Insect Communication — Chemical.*

Mano D. Pathak, International Rice Research Institute, Philippines: *Patterns of Interaction between Plants and Insects.*

T. R. E. Southwood, Imperial College Field Station, Ascot, England: *The Dynamics of Insect Populations.*

Powers Messenger, University of California, Berkeley: *Parasitoids, Predators and Population Dynamics.*

Waldemar Klassen, U.S.D.A., ARS-Plant Industry Station, Maryland: *Pest Management — Organization and Resources.*

L. Dale Newsom, Louisiana State University: *Pest Management — Concept to Practice.*

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—*Editor*

NOTES ON NECROPHORIC BEHAVIOR IN THE ARCHAIC ANT *MYRMECIA VINDEX* (FORMICIDAE: MYRMECIINAE)*

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Introduction

Ants of the Australian and New Caledonian genus *Myrmecia* apparently include the most archaic living Formicidae. Brown (1954) suggested that the genus may represent a relatively late evolutionary offshoot, specialized but fundamentally conservative, from a line of extremely generalized archaic forms represented as fossils by the genus *Prionomyrmex* of the Baltic amber and by the living Australian *Nothomyrmecia macrops,* of which only two workers have ever been found. Species of *Myrmecia,* therefore, may well illustrate the earliest patterns of Formicid social organization, and embody the most archaic patterns of Formicid social behavior, that we are likely to be able to study in detail in the laboratory or the field.

The bodily habitus of *Prionomyrmex* and *Nothomyrmecia* — not to mention of the far more archaic Mesozoic fossil genus *Sphecomyrma* first described by Wilson, Carpenter, and Brown (1967) which may well represent, as Wilson (1971) suggests, an antecedent of the Myrmecioid complex of ants — all suggest active, epigeically foraging insects: a characteristic virtually universal in contemporary species of *Myrmecia.* This, combined with the fairly large size of the communities of many species of *Myrmecia* — specific counts of 1586 workers and over 2000 in total colony personnel have been made from larger colonies of *M. gulosa* (Haskins and Haskins, 1950) — raise the interesting question of how far these archaic forms may have evolved any pheromone-mediated patterns of community-integrating behavior so conspicuous in many higher ants. This is an interesting and complex area of inquiry, the answers to which are far from obvious, as the recent investigations of Robertson suggest.

A prior question may be significant in this context. Do ants of the genus *Myrmecia* exhibit characteristic behavioral responses to particular chemical substances normally encountered in the external

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environment: substances which commonly evoke specific behavioral responses in higher ants? And if so are the responses elicited in *Myrmecia* essentially like those of higher ants?

We have recently described one such set of reactions: the stimulus to attack behavior in *Myrmecia gulosa* elicited by formic acid, a normal exocrine defense product of its common prey-genus *Camponotus,* but not, so far as can be determined, of *M. gulosa* itself (Haskins, Hewitt, and Haskins, 1973). The present investigation is concerned with the reactions of workers of a species of *Myrmecia* to substances which commonly stimulate necrophoric behavior in higher ants, such as oleic and related fatty acids.

Wilson (1958) and Wilson, Durlach, and Roth (1958) demonstrated that when groups of workers of the Myrmicine ant *Pogonomyrmex badius* come into contact with formic acid, ethylamine, triethanolamine, phenol, n-butyric acid, n-valeric acid, n-caproic acid, or n-caprylic acid, absorbed on centimeter-square patches of filter paper, they exhibit weak to moderate alarm behavior, sometimes passing into digging behavior, concentrated about the squares. In the case of oleic acid — and of that substance alone — the ants transported the paper squares away from the nest to the kitchen middens. A fatty acid component — quite probably oleic acid — obtained from the decaying bodies of *P. badius* workers also elicited necrophoric behavior in *Solenopsis saevissima.*

Blum, Doolittle, and Beroza (cf. Blum, 1970) fractionated dead workers of *Solenopsis saevissima* and determined that the releasers of necrophoric behavior were restricted to the rich free fatty acid fractions. Myristoleic, palmitoleic, oleic, and linoleic acids were present in these fractions, and all these acids possessed necrophoric activity in this species.

Such a reaction to chemicals like oleic acid has obvious adaptive advantage for any ant, or indeed for any social insect inhabiting a closed nesting situation. Such chemicals can serve as sensitive "indicators" of objects in the nest — whether prey or remains of adult or immature members of the community — which are dangerously decomposed and should be removed. It seems plausible, therefore, that this behavior pattern may have been established very early in the social evolution of the Formicidae. Hence it seemed of particular interest to investigate it within the Myrmeciinae.

Necrophoric Behavior in *Myrmecia vindex*

The species *Myrmecia vindex* was chosen for several reasons. It is a common and wide-ranging form in western Australia, where

it prefers open, partially xerophytic woodland habitats, but ranges much further, to South Australia and probably New South Wales and Victoria as well. It is an unusually hardy species and its colonies can be maintained in laboratory culture for many years. The primary reason for choosing it for this investigation, however, was that, in the populations from which nests were selected for both field and laboratory work, even mature colonies are typically quite small.[1] This and other characteristics suggest that the species is one of the socially less-evolved members of the genus and thus lend particular interest both to the reactions of its workers to necrophoric substances and to pheromones of higher ants.

Laboratory Tests

Reactions of workers of *Myrmecia vindex* to Oleic Acid

A portion of a colony of *M. vindex* consisting of approximately 30 workers, 20 cocoons, and 25 larvae, collected at Kings Park, Perth, West Australia, on December 28, 1961, and long established in the laboratory in an earth-containing Lubbock type glass nest of dimensions 7″ × 12″ and ¾″ in depth, was set up in a foraging arena consisting of a rectangular plastic box, 48″ × 24″ × 6.5″ in inside dimensions, to which the ants had free access. The bottom of the arena was covered with clean brown paper.

After the colony had become thoroughly conditioned to the environment, piles of brood which had been impregnated with 1 to 2 drops of various substances were placed on cardboard sheets, 6″ × 8″, at some distance from the nest entrance. There was early indi-

[1]Counts of four completely excavated apparently mature colonies from this population were made in January, 1964, with the following results:

Colony 1	1	typical brood female
	21	callow subalates (apparent female-worker intermediates)
	211	workers
Colony 4	1	typical brood female
	176	workers
Colony 6	1	typical brood female
	187	workers
Colony 7	1	typical brood female
	149	workers

This compares with a population count of a study nest of *M. vindex* reported by Douglas and McKenna (1970) as follows:

1	typical brood female
38	alate virgin females
38	dealate virgin females
210	workers
224	males

cation that larvae were only marginally suitable for this work. Treated larvae were sometimes returned to the nest, as though larval odor, even when overlaid by that of oleic acid, still dominated behavior. With cocoons, however, worker reactions were more consistent.

At 5:30 p.m. two piles of 10 larvae and 10 cocoons each were placed on top of the Lubbock nest. The larvae were quickly restored to the nest. By 6:15 p.m., 5 cocoons of the untreated group had been transported to the nest, together with 3 from the fraction treated with oleic acid. By 6:38 p.m. all cocoons from the untreated pile had been transported to the nest, while no further oleic-acid-treated cocoons had been removed. By 8:55 the following morning, however, 4 of the oleic-acid-treated cocoons had been deposited in refuse middens in the arena, 2 being deposited 45″ from the nest entrance and 2, 10″ away. Three were still in original position on the cardboard, but had been well covered with earth. Earth grains obtained from inside the nest had also been deposited on spots of oleic acid which had drained from the cocoons to the cardboard.

The experiment was then repeated more precisely in the pattern of the work reported with *P. badius*. Ten squares of paper, ½″ × ½″, were soaked with oleic acid and scattered at random over the surface of the nest, together with 10 identical but untreated squares, appropriately identified. Two larvae, likewise treated with oleic acid, were included. The trial was begun at 9:10 a.m.

Workers coming into contact with the treated objects immediately executed marked cleaning movements and a rubbing of the gular surface of the head against the substrate. At 9:20, 1 larva was picked up by a worker after much hesitation and held in the mandibles for 4 minutes, when it was grasped by a second, and then deposited by both at the nest entrance, but not taken inside. The impression of a conflict of drives was strong. One minute later this larva was again picked up, carried about 3″ from the nest entrance, and dropped. By 9:53, it had been brought into the nest, while the second larva was held within ½″ of the nest entrance. Two minutes later it also was brought into the nest.

At 10:00 a.m. a worker was beginning to deposit earth grains on the oleic-acid-treated papers, and by 10:53, 4 papers carried earth grains. By 1:00 p.m., one of the treated larvae had again been brought out of the nest, and a worker was preparing to drop it on the midden located 45″ from the entrance. By 5:00 p.m. both treated larvae were on this midden. Burying of the oleic acid squares continued but they were not moved toward the middens.

At 5:10 p.m., 2 Tenebrionid larvae, 1 treated with oleic acid and the other untreated, were placed outside the nest entrance. At 5:13 p.m. the untreated larva was carried into the nest, and 1 minute later the treated larva also was seized and carried in. At 5:30 p.m., however, the treated larva was brought out, carried to a distance of 34″, and discarded. The untreated larva was retained within the nest and shortly consumed.

These trials gave strong evidence that patterns both of burying and of rejection of objects impregnated with oleic acid are exhibited by *M. vindex*. It then seemed of interest to compare the reactions to oleic acid with those of other substances tested by Wilson *et al.* in their work with *P. badius*.

Reactions of workers of *Myrmecia vindex* to Methyl benzylamine; Caproic acid; Oleic acid; Formic acid

Using the same colony and with the same experimental arrangements as above, 14 cocoons, ranging from freshly spun to nearly ready to eclose, were impregnated as follows:

Methylbenzylamine (3 drops)	3 cocoons
Caproic acid (3 drops)	3 cocoons
Oleic acid (3 drops)	3 cocoons
Formic acid	3 cocoons

2 cocoons were retained as controls.

All these cocoons were placed on cardboards, and mounted on top of the Lubbock nest as before, at 2:04 p.m.

At 2:19 p.m. the 2 controls and the 3 cocoons treated with formic acid had been permanently returned to the nest. At 5:40 p.m., 1 cocoon from the caproic acid group had been removed 40.5″ from the nest and deposited on a refuse midden. All other cocoons remained untouched.

At 8:45 a.m. on March 31, no further cocoons had been removed from the cardboards, but a few grains of earth had been deposited on the cardboards of the caproic- and oleic-acid treated objects. During the night the caproic-treated cocoon deposited on the refuse midden had been retrieved into the nest, but at 8:55 a.m. it was again brought out and carried to the midden, 44″ from the nest entrance. Almost immediaeely it was again retrieved and returned to the nest. At 9:10 a.m., it was once more removed and dropped about 9″ from the nest entrance. By 2:03 p.m. this cocoon had been carried to a midden 36″ from the entrance, but 1 minute later

it was returned to the nest once more, only to be finally removed by 2:33 p.m. and dropped about 32″ from the nest entrance. At this time the 3 cocoons treated with oleic acid, the 3 treated with methylbenzylamine, and the remaining 2 treated with caproic acid were still in place on the cardboards, and a few grains of earth had been deposited about each. They were permanently ignored.

Reactions of workers of *Myrmecia vindex* to Triethanolamine: n-Valeric acid; Oleic acid

The same experimental arrangement was set up, using another colony of *M. vindex,* taken from the same population in Kings Park, Perth, West Australia, on January 10, 1965. Cocoons were treated as before:

Triethanolamine (3 drops)	3 cocoons
n-Valeric acid (3 drops)	3 cocoons
Oleic acid (3 drops)	3 cocoons

3 cocoons were retained as controls.

The 12 cocoons were arranged radially about the nest entrance, the control and the oleic acid groups furthest from it. Exposure was begun at 2:47 p.m.

Triethanolamine proved a powerful attractant, and the cocoons treated with it aroused immediate and intense attention. Within 3 minutes, 1 was dragged into the nest. At 2:51 a second triethanolamine-treated cocoon was dragged to the nest enerance and dropped. At 2:52 the third was carried to the oleic-acid-treated group outside the nest and dropped there. Two control cocoons were carried into the nest at the same time. A spot of triethanolamine stain on the containing card was repeatedly examined by workers.

The second triethanolamine-treated cocoon, which was deposited initially near the nest entrance, at 2:56 p.m. was carried to a midden 45.5″ away; it was then picked up almost immediately and redeposited at a distance of 40″. At 3:02 the triethanolamine-treated cocoon which had first been brought into the nest was taken out, carried to a point about 9″ away, and dropped. Earth grains had been deposited about the n-valeric acid group. The 3 oleic-acid-treated cocoons had not been moved nor buried. By 4:00 p.m. all three triethanolamine-treated cocoons had been discarded in a group 39″ from the nest entrance; 1 control cocoon was still in place; and all 6 cocoons treated with n-valeric and oleic acid remained in their initial position. At 4:50 p.m. there had been no further change and the run was terminated.

On April 2, 1965, the same experiment was repeated, substituting n-butyric for n-valeric acid. Results were essentially the same. Fifty-five minutes after the start, 3 of the 4 triethanolamine-treated cocoons had been transported for distances of 40″, 21″, and 25.5″ from the nest entrance and dropped; although none of the n-butyric or oleic acid cocoons had been moved, there was a considerable deposit of earth particles about them. One control cocoon had been moved about 2″, but none had been carried into the nest. Twenty minutes later, the triethanolamine group was still being moved at frequent intervals, and the oleic acid group was being heavily banked with earth grains. No attention was paid to the n-butyric acid groups.

The strong impression left by these trials, and others like them, was that oleic acid, and to a lesser degree caproic acid stimulate in *Myrmecia vindex* both a burying reaction and sometimes the transport of objects so contaminated to refuse middens. No evidence of overt digging was seen. Formic acid seemed without effect. Triethanolamine, however, functioned as an efficient excitant and attractant in higher concentrations. In lower concentrations it stimulated necrophoric behavior. The "conflict" behavior exhibited in the handling of some larvae and cocoons treated with several of these substances, when immatures were repeatedly taken into the nest, brought out again and discarded on a midden, then returned to the nest, sometimes through three or four cycles, was in several cases striking.

Field Tests

Reactions of workers of *Myrmecia vindex* to Oleic acid; Caproic acid; Formic tcid; Methylbenzylamine

It was of interest to conduct essentially similar tests with wild colonies in the field. A large and active colony of *M. vindex* in Kings Park, Perth, West Australia (a part of the same population from which the colonies had been taken for laboratory tests), was selected. It included approximately 200 workers, had a single large entrance-hole, and a well-defined crater. Since workers of this population show a predominantly crepuscular and nocturnal foraging pattern in warm weather, tests were begun in the evening.

At 7:25 p.m., as dusk was gathering, 5 white cards, of dimensions 3″ × 5″, were mounted on the nest crater, approximately equidistant from the entrance. Twenty-five cocoons, obtained from a neighboring colony, were impregnated with 3 drops of test substance, with 7 retained as untreated controls. The arrangement and treatments were as shown below:

Card Marking	*No. of Cocoons*	*Substances Impregnated*
C	7	Caproic acid
F	6	Formic acid
M	7	Methyl benzylamine
O	5	Oleic acid
L	7	Control

Immediately on exposure a worker on the crater seized one control and dragged it inside the nest. A second worker, encountering an oleic-acid-treated cocoon, started away. At 7:32, 1 caproic-acid-treated cocoon was dragged into the nest, followed at 7:35 by a second control cocoon. At 7:37 a cocoon from the formic acid group was taken to the nest. Between 7:37 and 7:40, 3 additional formic-acid-treated cocoons were taken into the nest, and one-half minute later the last control cocoon was taken in. One of the remaining two formic acid cocoons was inadvertently toppled into the nest by another worker, leaving 1 on the card. The other groups were untouched. At 8:02 p.m., when darkness forced cessation of observation, all cocoons treated with oleic acid, methylbenzylamine, and five of those with caproic acid remained in place on the cards. One cocoon treated with caproic acid had been deposited with the oleic-acid-treated group.

At 6:00 a.m. the following day, 3 of the caproic-acid-treated cocoons had been removed, but it was not possible to determine whether they had been taken into the nest or discarded. Some grains of earth had been scattered on the caproic-acid-treated card.

Observations were continued throughout the day, but no further attention was paid to the remaining cocoons. However, when the cards were removed from the crater at 7:00 a.m. on the third day, it was found that a new entrance-hole had been excavated under the card carrying the oleic-acid-treated cocoons.

It was clear that oleic acid, caproic acid, and methylbenzylamine effectively inhibited return of the cocoons to the nest by the workers, in marked contrast to those treated with formic acid and the controls, which were brought in promptly. Digging behavior was observed in the vicinity of oleic acid. In these experiments, however, the oleic acid objects were not buried nor transported to kitchen middens — perhaps because such middens of *M. vindex* are often located near the nest entrance. Indeed, it is an interesting behavioral characteristic of *M. vindex,* at least in this population that, at the seasons of maximum brood production, empty cocoons and pupal exuviae are frequently piled near the nest entrance. That this disposition may be more than accidental is suggested by the behavior of some colonies

in the laboratory (not those with which the above-mentioned tests were conducted), where such exuviae, originally scattered about a foraging arena, may be gathered into dense craters about the entrances to Lubbock nests.

Summary and Conclusions

In a parallel series of experiments to those reported by Wilson (1958) and Wilson, Durlach, and Roth (1958) with *Pogonomyrmex badius,* the effects of oleic acid, caproic acid, methylbenzylamine, n-butyric acid, n-valeric acid, formic acid, and triethanolamine as behavioral releasers in the ant *Myrmecia vindex* were investigated both in the laboratory and the field. The comparison was deemed particularly interesting because of the archaic character of the Myrmeciinae and their societies.

As with *Pogonomyrmex* and other higher Formicid genera, oleic acid was found to act as a releaser of both necrophoric and digging behavior, suggesting the early establishment of this set of reaction patterns in Formicid social evolution — a not unexpected situation in view of the highly adaptive character of this pattern in ridding the nests of dangerous animal decomposition products, perhaps in response to the bacterial production of oleic and related fatty acids. In *Pogonomyrmex,* n-butyric acid, n-valeric acid, and n-caproic acid stimulated weak to moderate alarm behavior, passing over into digging behavior. In *Myrmecia,* caproic acid stimulated mildly necrophoric behavior, associated with some digging and burying behavior. Exposure to filter papers of cocoons impregnated with n-butyric acid resulted in deposition of earth grains on the treated object. No reaction was observed to n-valeric acid.

Thus responses to these substances were of the same general quality as those reported for *P. badius.* There were, however, very marked differences in the responses of *M. vindex* to two presumed releasing substances: formic acid and triethanolamine. Formic acid neither stimulated necrophoric nor digging behavior nor prevented immediate transport into the nest of formic-acid-treated cocoons. This result was somewhat surprising to the authors in view of the highly positive and specific attack reactions stimulated by formic acid in *Myrmecia gulosa* mentioned earlier, which have been reported elsewhere (Haskins, Hewitt, and Haskins, 1973). The most marked contrast between behavior patterns of *P. badius* and *M. vindex,* however, occurred with those released by triethanolamine. With *M. vindex,* vapors of this compound consistently stimuated the most conspicuous necrophoric behavior of any substance tested, while also acting as a

decided attractant. In *P. badius* on the contrary, the reaction to triethanolamine was reported to be virtually neutral.

In this connection it is interesting to note that, in the populations studied, *M. vindex* commonly piles discarded cocoons and pupal exuviae on the crater of the nest, near the entrance, where they characteristically accumulate in some numbers, rather than transporting them far afield. Similar behavior has been described for *P. badius* (Wilson, Furlach, and Roth, 1958), though in the latter case, removal of the discards is quickly accomplished by other foraging ants. The situation with *M. vindex,* however, appears more specific. Indeed established colonies in the artificial nest may collect discarded cocoons and pupal exuviae scattered about the foraging area to form a crater about the entrance. It may be that subtle behavioral balances are involved, depending on the nature and "mix" of the included decomposition products, as suggested by the reversal of behavior, apparently in response to vapor concentration, released by triethanolamine.

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THE FIRST RECENT SPECIES OF *PROTOMUTILLA* (HYMENOPTERA: MUTILLIDAE; MYRMOSINAE)[1]

By Denis J. Brothers[2]

During a recently completed study of the higher classification of the aculeate Hymenoptera (Brothers, 1974), my attention was drawn to a female specimen from India representing a species of Myrmosinae (considered a subfamily of Tiphiidae by many authors, e.g., Krombein, 1940) but showing marked similarities to *Nanomutilla* (a member of the Mutillidae often included in the Myrmillinae). This situation is reminiscent of that found by Bischoff (1915) for seven female specimens in Baltic amber. All of these have the well-developed pro-mesonotal suture characteristic of the Myrmosinae, but in addition "die Tiere weisen Beziehungen zu verschiedensten Gattungen auf, so zu *Myrmilla, Nanomutilla, Mutilla* s. str. etc." Bischoff described the genus *Protomutilla* to include these seven species, and considered it best placed in the "Mutillinae", although intermediate between this taxon and the "Myrmosinae" (which he considered to be a member of the Mutillidae). He listed the most characteristic features of the genus as: the distinctly developed pro-mesonotal suture, the transverse first abdominal (metasomal) segment, the lack of a pygidial area, the usually longitudinally striate sculpturing of the mesonotal region, and the absence of long pubescence. In addition, all of his specimens have the posterolateral angles of the mesosoma acute or dentate. The Indian specimen possesses all these characters except for that of the mesonotal sculpturing (absent in some of Bischoff's species also). The form of the posterolateral angles of the propodeum differentiates this genus from the others with a well-developed pro-mesonotal suture, so that the Indian specimen seems best considered to represent a modern species of *Protomutilla.* Placement of this genus in the Myrmosinae is supported by the almost straight and well-differentiated hind margin of the pronotum and also by the presence of a well-developed carina dorsally on the hind coxa (a character not mentioned by Bischoff), although this is not as markedly lamellate as in most other myrmosines.

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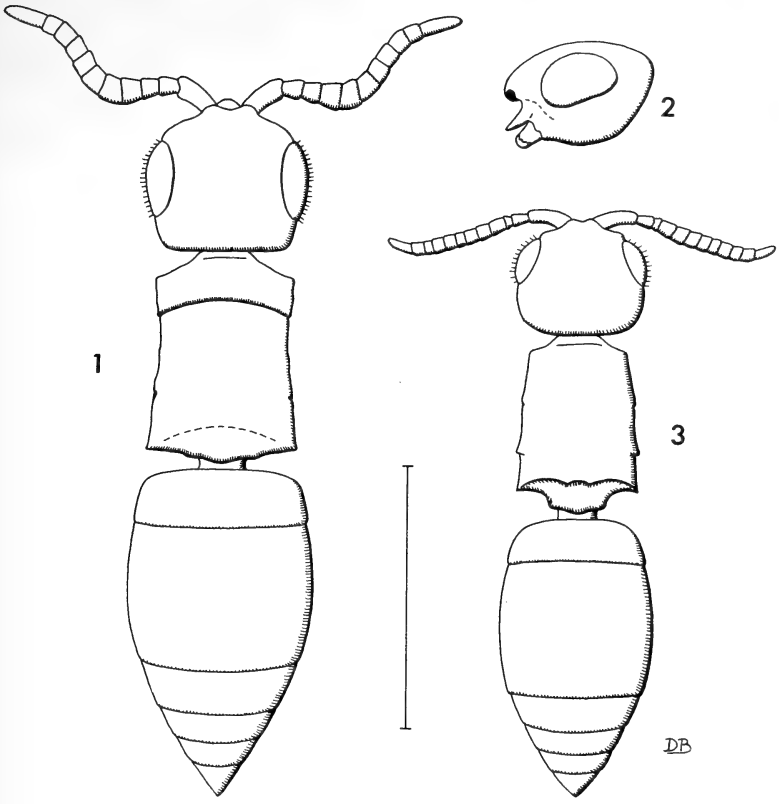

Figs. 1-2. *Protomutilla microsoma,* sp. nov., ♀. 1, dorsal view, legs omitted; 2, head, lateral view, antenna and palpi omitted. Fig. 3. *Nanomutilla microsoma* André, ♀, dorsal view, legs omitted. Scale = 1.0 mm.

Protomutilla microsoma sp. nov.

(Figs. 1-2)

FEMALE: Length 2.6 mm. Body finely and evenly punctate with sparse, short, pale pubescence; black except clypeus, antennal tubercle, antenna, mandible, ventral third of pronotum laterally, legs, fifth and sixth metasomal segments and apical margins of other metasomal segments testaceous, and palpi stramineous. *Head* almost prognathous, 1.1 times as wide and 0.7 times as high as long, 1.1 times as wide as mesomoma; sides weakly converging behind eye, about 0.3 times length of eye; ocelli absent; eye broadly oval, with many short setae; frons evenly swollen, produced between barely differentiated antennal tubercles; malar space 0.4 times as long as eye; weak genal carina present; clypeus flattened, anteriorly produced with strongly convex apical margin; antenna with scape 3.0 times as long as wide, pedicel about as long as first flagellar segment which equals second in length, flagellum widest at third segment; mandible approximately parallel-sided, obliquely tridentate, the apical tooth strongest. *Mesosoma* 1.4 times as long (excluding anterior collar) as wide; width at humeral angle 0.9 times that at propodeal angle. Pronotum (excluding collar) 0.3 times as long as wide; hind margin shallowly concave; lateral margins slightly convergent posteriorly; humeral angle pronounced. Mesonotum approximately parallel sided, 0.9 times as wide as pronotum. Propodeum with lateral margins divergent posteriorly, forming a strong dentiform angle on each side; disc and declivity barely differentiated. Mesosomal pleura differentiated from nota by a longitudinal carina; concave except convex posteriorly forming propodeal angle. *Legs* unmodified; foretarsus without spines (i.e., pecten undeveloped); hind coxa with obtuse lamellate tooth dorsally; hind tibia without spines externally, only a very few minute spines apically. *Metasoma* about 1.7 times as long as wide, 1.25 times as wide as mesosoma; first tergum 0.4 times as long as wide, about as wide as and 0.4 times as long as second; sixth tergum sparsely punctate, without differentiated pygidial area; first sternum with single blunt anteriorly-directed midventral tooth.

MALE: Unknown.

HOLOTYPE: ♀, [India, Orissa Prov.], Nilgiri Hills, 3500 ft. (H. L. Andrewes); in Hope Department, University Museum, Oxford, England. (No date of collection given.) The specimen is unfortunately damaged, and lacks the apical three segments of the left foretarsus, the left mid- and hind and right mid-tibiae and tarsi; the left antenna is glued to the card bearing the "minuten"

pin. Since the specimen has been remounted from a glued card mount, some features of the venter and appendages remain somewhat obscured by glue.

Although Bischoff's (1915) descriptions are very short, *P. microsoma* seems clearly to differ from all the amber species. It may be most similar to *P. nana,* but the head undoubtedly differs in form from that species.

The resemblance of *P. microsoma* to *Nanomutilla* (Fig. 3) is quite remarkable, the most basic difference being the form of the pro-mesonotal suture. In addition to gross body form, these species have highly similar coloration and puncturation, and all are rather small in size. *Nanomutilla* even has a weakly developed carina on the hind coxa as well as pubescent eyes, characters lacking in the higher Mutillidae. These marked similarities tend to support my conclusions (elaborated in Brothers, 1974) that the Myrmosinae should be considered a subfamily of Mutillidae.

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LIFE HISTORY OF *ABEDUS HERBERTI* IN CENTRAL ARIZONA (HEMIPTERA: BELOSTOMATIDAE)*

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Introduction

Torre Bueno in 1906 noted the meagerness of information on the biology and immature stages of aquatic Hemiptera. Although this condition has changed somewhat in the more than 60 subsequent years, complete life histories for representatives of only two of the five genera belonging to the subfamily Belostomatinae (Lauck and Menke 1961) are available. *Belostoma* is represented by *B. flumineum* Say (Torre Bueno 1906), *B. oxyurum* (Dufour), *B. bifoveolatum* Spinola (Schnack 1971), and *B. malkini* Lauck (Cullen 1969). The Old World genus *Limnogeton* is represented by *L. fieberi* Mayr (Voelker 1968). Menke (1960) was successful in bringing a single individual *Abedus dilatatus* (Say) to its fifth instar, at which time it died. Life histories for representatives of the genus *Lethocerus* include: *L. americanus* (Leidy) (Rankin 1935), *L. cordofanus* Mayr (nec. *L. niloticus* Stål) (Tawfik 1969), *L. mazzai* De Carlo (De Carlo 1962), and *L. maximus* De Carlo (Cullen 1969). Nothing is known of the immature stages of *Horvathinia* (subfamily Horvathiniinae, Lauck and Menke 1961). The taxonomy and distribution of *Abedus herberti,* as well as a behavioral and ecological sketch of the genus, is provided by Menke (1960).

Methods and Materials

I collected adult bugs, including males encumbered with eggs, with the aid of a gasoline lantern at night from the following central Arizona localities: Sycamore Creek, Maricopa County, near Sunflower; Camp Creek, Maricopa County, near Carefree; and Tule Creek, Yavapai County, in the Bradshaw Mountains.[1] Plastic bags containing stream water isolated individuals for transport to the

[1]Menke's 1960 revision recognizes polytypy in *A. herberti.* The central Arizona specimens studied in this paper belong to "subspecies *herberti*" in contradistinction to "subspecies *utahensis.*"

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laboratory. Plastic washbasins (15 by 26 by 30 cm) containing clean gravel and deionized water housed bugs in the laboratory. Finger bowls (10.5 by 4.5 cm), provided with aquarium gravel and deionized water to a depth of about 4 cm, received hatchlings obtained from eggs of field-captured encumbered males. Gravid females, paired with unencumbered males, produced fresh eggs for incubation studies. First and second instar nymphs were fed on cultured vestigial winged *Drosophila* which were floated on the water's surface. Third and fourth instars received legless crickets (*Acheta domestica*), and fifth instars ate intact crickets. I renewed food and water every other day, and recorded molts which had occurred each day. Cast skins were preserved in seventy percent alcohol, one percent glycerin for study and measurement. Open water temperature in the laboratory was a reasonably constant 18 C (± 0.5 C).

I observed hatching and used still and motion picture photography to record this event for analysis. I measured eggs, first, second, and third instar nymphs and the legs of fourth and fifth instars using a stereoscope ocular micrometer, and the bodies of fourth and fifth instars with a dial caliper.

Eggs, Incubation, and Hatching

EGGS

The eggs of *Abedus* are always laid on the back of the male (Fig. 1A). Oviposition, which continues for 12-48 hours in the laboratory, alternates with copulation. Encumbered males are found throughout the year in Arizona. A detailed study of courtship and male brooding behavior in *A. herberti* will be presented elsewhere (Smith, in prep.).

A mucinous glue is secreted by the female prior to the deposition of each egg starting at the apex of the male's hemelytra and proceeding forward, uniformly covering the male's back up to and sometimes including the pronotum. It is usually the case that males carry the eggs of only one female, but polygynous matings apparently do occur (Menke 1960). I inferred from data on hatching, that of seven encumbered field captured males, only one individual had consorted with two females to acquire his load of eggs. In this instance, 72 eggs hatched over a five day period, this followed by three days during which no eggs hatched. The remaining 15 eggs hatched over a 24 hour period. In all other cases, hatching occurred more or less continuously over a three to five day period.

Freshly laid eggs begin swelling immediately. Swelling has the

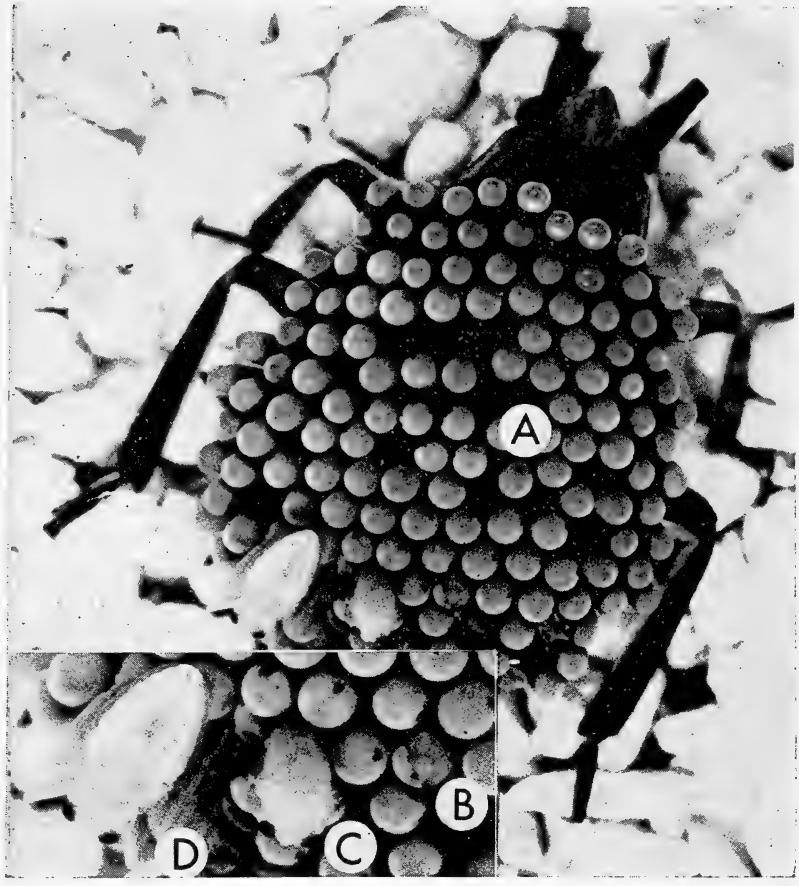

Figure 1. Encumbered male *Abedus herberti* and hatching of eggs.
A. Encumbered male *Abedus herberti*.
Inset. Enlargement of hatching nymphs.
B. Rupture of the chorion around cap.
C. Resting position.
D. Newly emerged nymph.

ultimate effect of compacting the mass, enhancing its structural integrity and conformity to the male's back. The resulting gelatinous plate with its embedded eggs is strong, flexible and adheres tenaciously to the male's hemelytra so long as it is kept moist. If exposed to air for 60 minutes or longer, the gelatinous pad becomes brittle, loses its adhesive properties and on prolonged exposure will eventually fall off.

Eggs increase in size from mature oviducal (3.064 ± .022 mm by 1.732 ± .017 mm, n = 50) to those containing nymphs ready to hatch (4.983 ± .036 mm by 2.001 ± .017 mm, n = 50). This represents a 59 percent mean increase in length and a 15.5 percent mean increase in width. The initial swelling of the egg (during the first 48 hours) may be due to imbibition of water, however later increase in size seems to be due to the development of the embryo. Both Hungerford (1925) and Tawfik (1969) noted dramatic increases in egg size during the development of *Lethocerus* eggs which are laid above the water on emergent vegetation. Cobben (1968) provides a synthesis of what is known about belostomatid eggs and embryology.

Mature oviducal and freshly laid eggs are variable in shape, usually imperfect oval with one nearly straight side, yellow in color and irregularly hexagonal microreticulate. Soon after occlusion, eggs darken to tan. The cap (upper ⅓) differentially darkens and remains several shades darker until just prior to eclosion of the nymph at which time it becomes grayish white in color. As development proceeds the shape of the egg comes to resemble an elongate "printed comma"; that is broad and rounded at the free end, narrow and pointed at the attached end, with one convex and one concave side. The concave side seems always to face the posterior of the mass. Cobben (1968, Fig. 232) shows the head of the embryo (of *Sphaerodema* = *Diplonychus*) facing the attached end, but embryonic rotation must occur prior to hatching. I observed one instance of egg failure due to nonrotation of the embryo.

INCUBATION

Male brooding of eggs, a complex of behaviors, is necessary for achievement of the greater than 95 percent survival observed for eggs of field-captured encumbered males. I never observed any type of egg parasitism. Egg failure, in every case but the one, seemed due to insemination failure; usually a few eggs on each plate did not develop. Open spaces in the laying pattern in Figure 1A are undeveloped eggs. Harvey (1906) reported that infertile eggs of *Pedino-*

Table 1. Mean intermolt times (days) for laboratory reared nymphs of *Abedus herberti*.

	$\bar{x}$	n	Range	Confidence limits on population mean*
Hatch to 1st molt	8.8	31	7-13	$7.6 - \bar{x} - 10.0$
1st molt to 2nd	8.9	30	7-12	$7.1 - \bar{x} - 10.6$
2nd molt to 3rd	9.0	30	7-13	$7.4 - \bar{x} - 10.7$
3rd molt to 4th	11.3	26	11-14	$10.4 - \bar{x} - 12.3$
4th molt to 5th	20.4	26	18-31	$17.8 - \bar{x} - 23.0$

*Confidence level 99.999

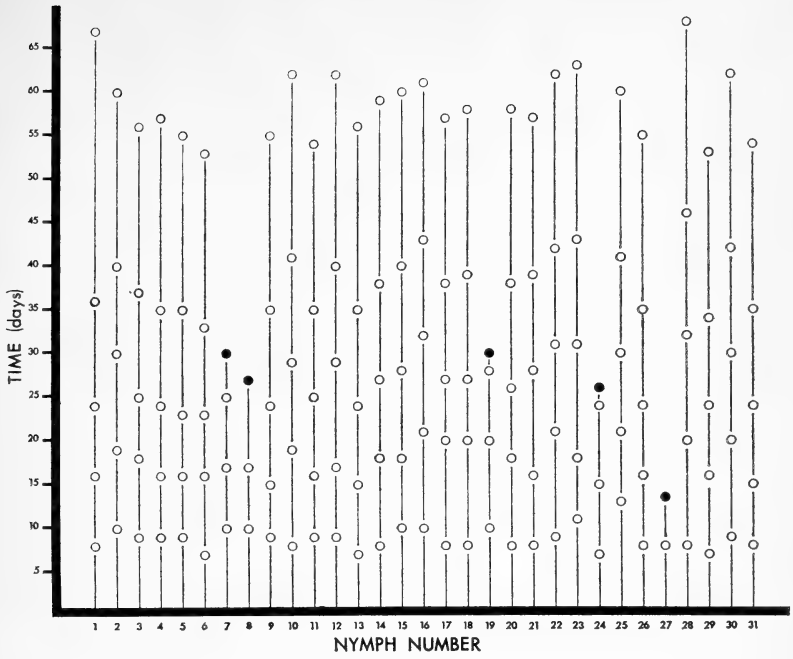

Figure 2. Individual molt records for 31 laboratory reared nymphs of *A. herberti*. Open circles indicate molts. Closed circles indicate the death of that nymph.

coris macronyx (= *Abedus indentatus* Haldeman) drop off and are replaced (presumably by the original or another female) by others as late as the sixth or eighth day of incubation, but in every instance I observed, nonviable eggs were retained in the nidus through incubation and hatching of the viable eggs. Incubation periods from laying of the first egg to hatching of the first ranged from 21 to 23 days in the laboratory. Voelker (1968) has shown developmental time for eggs of *Limnogeton fieberi* to be directly correlated with temperature, the optimal temperature being 32-33 C. He reports an 8 day development time at optimal temperatures, which seems to be more in agreement with the results obtained by the majority of other workers for belostomatids (Torre Bueno 1906, Harvey 1906, Hungerford 1925, and Tawfik 1969). Menke (1960) found the incubation time for *A. dilatatus* to exceed 30 days in the laboratory, but we both (Menke, personal communication) suspect that development

of eggs for *Abedus* could be substantially accelerated by increasing the temperature of the incubation water. Open water temperature in my laboratory (18 C) fell within the range of spring, fall and winter stream temperatures in Arizona.

HATCHING

Twenty-four hours prior to hatching, the free end of the egg swells dorsally. Pressure from within eventually causes a rupture in the chorion around the cephalic cap (Fig. 1B). Invariably, nymphs hatch facing the brooding male's posterior. I can't explain this constant orientation of hatching nymphs, but its effect is that adjacent eggs can hatch simultaneously with a minimum of interaction between eclosing nymphs. The cap is lifted by the head as the nymphal thorax emerges, but remains hinged to the egg on the side of the latter which faces the ventral surface of the emerging nymph. The nymph's head slips from under the operculum as peristaltic contractions free one half of the body. When the nymph is two thirds removed, it rests in a position perpendicular to the plane of the egg plate (Fig. 1C). Moments later it arches backward and stretches its legs which are employed in final extraction when the nymph again leans forward. A newly emerged bug generally lingers on the back of the male for several minutes to inflate its laterally constricted abdomen (Fig. 1D). This accomplished, it moves off in search of cover among aquatic plants or debris where it assumes the predatory stance characteristic of nymphs and adults alike. Freshly emerged nymphs are light honey yellow in color and translucent, but darken within one hour.

Nymphal Development and Nymphs

DEVELOPMENT

Of 31 nymphs reared in the laboratory, 26 survived to adulthood. Individual developmental records are illustrated in Fig. 2 and mean developmental periods are presented in Table 1. These results compare favorably with those of Voelker (1968) for *Limnogeton* and probably reflect critical minimum periods required for morphogenesis between molts under optimal conditions. That availability of food is an important factor related to intermolt time for these sedentary hunters was demonstrated in a simple experiment. Ten of 20 sibling first instars, fed *Drosophila* daily, all molted in under eight days while the other ten, fed every fourth day, did not begin to molt until the nineteenth day. Thirty additional sibling first instars were di-

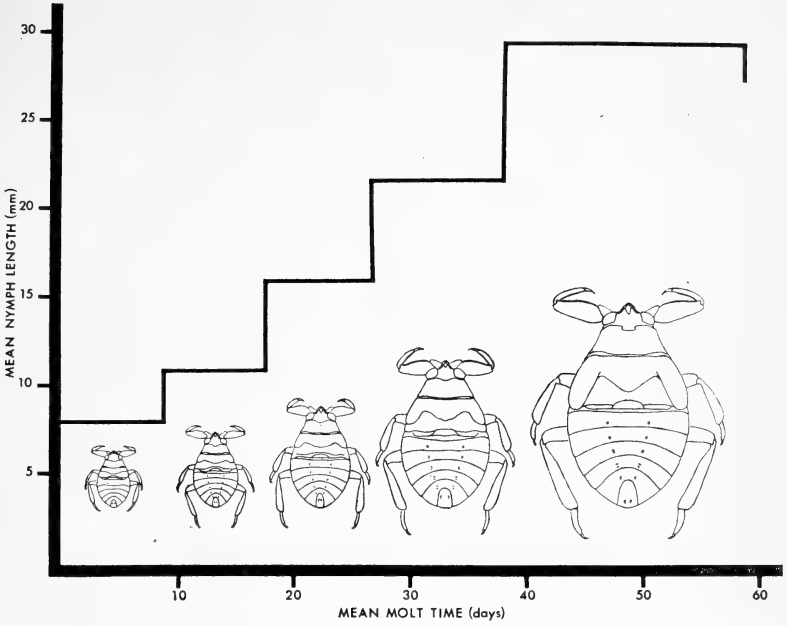

Figure 3. First through fifth instar nymphs of *A. herberti.* Mean length and mean duration of instars illustrated graphically.

vided into three groups of ten individuals. Each group was kept at a different temperature (18 C, 22 C, and 31 C) and all nymphs received *Drosophila* daily in numbers exceeding that which they could consume. All molted at approximately the same time (on the sixth or seventh day), suggesting that temperature is relatively unimportant. These experiments were not intended to be conclusive and it is probable that a food-temperature interaction could be detected with more sophisticated experimentation.

NYMPHS

There are five nymphal instars for *A. herberti.* Dorsal views of the five are figured (Fig. 3) and mean morphometric data for fifteen characters of each instar are presented in Table 2. The wide (.001) confidence limits around each mean should encompass interpopulation variation for central Arizona. Mean size of bugs seems to be stream specific, perhaps due to low dispersal of these animals and reduced gene flow between their populations. *A. h. herberti* intergrades with

Table 2. Confidence limits* on mean nymphal instar morphometry of *Abedus herberti*.

		Instar I	II	III	IV	V
Body	Length	7.857 ± .358	10.849 ± .984	14.964 ± 1.189	21.530 ± 1.231	29.470 ± 1.437
	Width	4.754 ± .288	6.844 ± .623	8.907 ± .543	12.755 ± .499	16.928 ± 1.309
Head	Width	2.474 ± .091	3.333 ± .310	4.278 ± .400	5.265 ± .362	6.670 ± .555
Leg I	Femur	2.456 ± .091	3.112 ± .217	3.911 ± .357	5.354 ± .750	7.229 ± .586
	Tibia	1.564 ± .876	2.076 ± .831	2.698 ± .200	3.586 ± .350	4.814 ± .499
	Tarsus	.612 ± .044	.692 ± .082	.822 ± .187	1.024 ± .100	1.328 ± .155
	Claw	.298 ± .050	.356 ± .104	.416 ± .060	.508 ± .036	.710 ± .118
Leg II	Femur	2.404 ± .111	3.226 ± .233	4.178 ± .358	5.883 ± .758	8.111 ± .917
	Tibia	2.046 ± .131	2.694 ± .142	3.588 ± .264	4.920 ± .657	6.981 ± .653
	Tarsus	.915 ± .125	1.118 ± .110	1.426 ± .194	2.007 ± .282	2.808 ± .291
	Claw	.304 ± .025	.410 ± .055	.583 ± .068	.736 ± .064	1.096 ± .119
Leg III	Femur	2.907 ± .122	3.901 ± .312	5.189 ± .532	7.306 ± .676	10.590 ± .838
	Tibia	2.977 ± .275	3.956 ± .220	5.293 ± .416	7.396 ± .926	10.992 ± .703
	Tarsus	1.214 ± .076	1.574 ± .147	2.074 ± .285	2.773 ± .310	3.956 ± .338
	Claw	.344 ± .049	.506 ± .033	.676 ± .072	.868 ± .098	1.252 ± .070

*Confidence level = 99.999 around means of measurements from 10 laboratory reared specimens.

a smaller subspecies *A. h. utahensis* in northern Arizona and southern Utah.

The first through the fourth instars all have two segmented antennae and one segmented pro-, and two segmented meso- and metatarsi. The beak is four segmented from the first instar to imago. One antennal segment is added in the fifth instar and usually another in the adult. All tarsi add one segment in the adult molt.

The most noteworthy changes through instars are the allometric development of the wing pads (Fig. 3) and of the protarsal claws. Torre Bueno (1906) states that there is a progressive diminution in size (through the instars) of the anterior (external) protarsal claw of *Belostoma flumineum* and that the external claw finally disappears in the adult. This statement is erroneous on at least one count, but nevertheless focuses attention on an ontological aspect of phylogenetic significance. It is now known (Lauck and Menke 1961) that both *Belostoma* and *Abedus* have vestigial external protarsal claws. The other three genera in the Belostomatinae have two well developed protarsal claws as does the genus *Lethocerus*. In *Abedus herberti,* and probably *Belostoma* as well, only the magnitude of the size difference between the external and internal protarsal claws increases with each molt due to nondevelopment of the external claw and continued growth of the internal. In the first instar relative length of the external claw is 50 percent of the internal. This is reduced to about 38 percent in the second, 30 percent in the third, 23 percent in the fourth, and 19 percent in the fifth instar. Curiously, in the adult the external is proportionally slightly longer than in the fifth instar and the internal claw is shorter and broader in the adult. This results in an increase in the relative length of the external claw to about 28 percent that of the internal in the adult bug.

Longevity

A. herberti is a relatively large animal and is a sedentary hunter, both of which characteristics suggest that it might be long lived. This seems to be the case; several specimens have lived in the laboratory for up to one year and one in particular, a female collected on October 14, 1972, lived until November 30, 1973 during which time she produced four sets of eggs totaling 344. Nymphs from the first through the third instars are probably subject to predation by other aquatic organisms. I have found first instar nymphs in the stomachs of trout taken at three forks of the Black River, Apache County, Arizona. Nymphal instars seem to play an important role in the

food economy of the species during periods of low stream productivity; I commonly find nymphs and adults feeding on smaller nymphs of their own species. After the second instar, cannibalism seems to be far the most common cause of fatality among nymphs. Ecdysal failure and physical catastrophes (flood and drought) also regulate populations. *Lethocerus* adults, which are seasonally common but never abundant in Sonoran streams, may regularly take adult *Abedus* but I have observed only one instance of this. In general, *A. herberti* adults are at the pinnacle of the aquatic food chain, and, having reached adulthood, stand an excellent chance of surviving to produce or brood several clutches of eggs.

Discussion

The life history of *Abedus herberti* seems to follow closely the pattern reported for other genera belonging to the subfamily Belostomatinae. Allometric development of the protarsal claws closely relates *Abedus* to *Belostoma,* and suggests their common ancestry with the two clawed genera. Five instars is the number characteristic of acquatic Hemiptera (Hungerford 1920).

Acknowledgements

I wish to thank Dr. M. Parsons, Dr. A. S. Menke, and Dr. J. Alcock for review.

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PREY CAPTURE BY *DRYMUSA DINORA* (ARANEAE, SCYTODIDAE)

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Introduction

The family Scytodidae includes at present three genera, of which *Scytodes* and *Loxosceles* are well known because of their specialized prey-capturing strategies. *Scytodes* species eject a sticky substance (perhaps similar to the silk from the spinnerets) from the chelicerae at a considerable distance to trap the prey (Bristowe, 1931; McAlister, 1960). The species of *Loxosceles* have developed a very effective venom capable of subduing strong prey almost instantly (Hite *et al.,* 1966). This venom affects even vertebrate tissues, including those of man (Bücherl, 1961).

The genus *Drymusa,* a small and poorly studied group, is morphologically more closely related to *Loxosceles* than to *Scytodes.* It lacks the high carapace, and possesses a colulus; also the male bulbus is located at the tip of the tarsus (Valerio, 1971). The forest-dwelling species of *D. dinora* Valerio, which lives exclusively under logs utilizing crevices and horizontal tunnels in the decomposed wood (Valerio, 1971), exhibits highly specialized behavioral patterns never observed in other spiders. The permanent web, composed of a few tangled threads, seems to alert the spider to the presence of prey and to restrict the movement of prey. Clearly, this type of construction represents a very primitive conditon in the phylogeny of the web (Kaston, 1966).

Materials

Several mature and immature specimens of *D. dinora,* of both sexes, were collected in a wet lowland forest in southwestern Costa Rica and kept individually isolated in 12-dram vials (100 × 22 mm), at 100 percent humidity and 24.5 ± 0.2°C.

Observations

This species is remarkable in two aspects of its attack behavior, departing from all known patterns: for large prey the spider spins

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a trap *after* the prey's arrival in the web, and prey-wrapping is carried out exclusively by movements of the abdomen and without using the appendages. Prey is treated in a different manner according to size and perhaps other qualities, as also occurs in other groups of web-building spiders (Eberhard, 1967; Robinson, 1969; Shear, 1969).

Attack on small prey: The spider rests in the center of the web (B in figure 1) near the superior edge of the crevice or tunnel. When small prey (less than ¼ the size of the spider) enters the tangled threads, the spider moves and attacks directly with the chelicerae and holds on firmly until the prey stops moving. Usually the prey is then carried to the resting site and feeding starts immediately without previous wrapping in silk. The arrival of a second item of prey does not elicit a response from the spider.

Attack on large prey: When large prey penetrates at one side (C in Figure 1), the spider runs to A and starts immediately spinning a horizontal partition. The prey then moves through the tangles of the center towards the trap web. If the prey cannot cross this barrier of dry silk and starts heading back, the spider moves ahead of it to C where it builds another vertical web, thus enclosing the prey in a silken trap. Then, the direct attack begins. The spider approaches its victim with certain caution and suddenly strikes five or six times with the chelicerae at intervals of one second. Sometimes, some chasing is involved. After the envenomation the prey may move around the web but the spider usually ignores it. Once the prey slows down (apparently due to the effect of the venom), it is wrapped in silk.

The silk is distributed by oscillatory movements of the whole body, reinforced by more pronounced side movements of the abdomen (with conspicuous flexions of the pedicel), changing position at intervals to deliver silk to different parts around the prey. No appendages (other than the spinnerets) are involved in the process. The prey is carried in the chelicerae to the upper portion of the web where wrapping continues for a few seconds. This post-immobilization wrapping seems to facilitate transportation of the prey to the resting site and attachment to the web for later feeding (Robinson *et al.*, 1969). Once the prey is wrapped, the spinnerets are carefully cleaned by back and forth movements of the distal third of the fourth metatarsus. Later, the fourth metatarsi, are, in turn, cleaned by the chelicerae.

Very large or very strong prey items entering the web do not produce an aggressive response from the spider. It simply lies flat

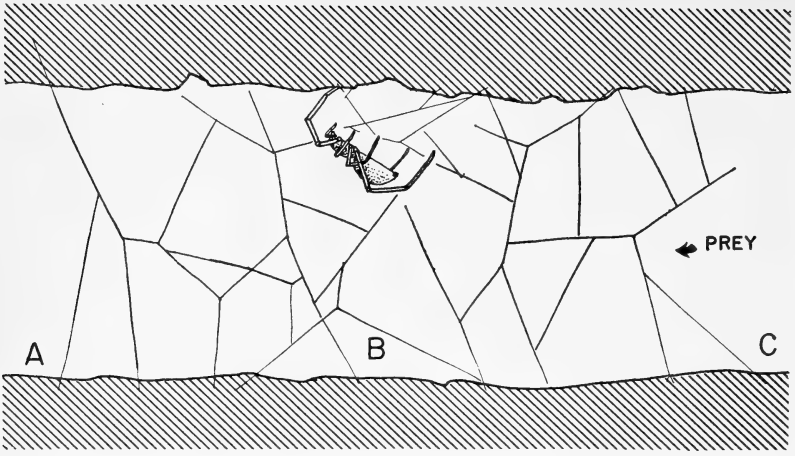

Figure 1. Spider *Drymusa dinora* in the resting area (B) in the center of the web. A trap is built at site A after prey enters through site C; later a second trap web is built at C to corral prey.

against the substrate while the prey passes through the area and moves on.

Females carry the egg-sac in their chelicerae much like the species of the genus *Scytodes* (and the structure of the sac itself resembles that of *Scytodes* also). The sac is temporarily abandoned when a suitable prey enters the web.

Discussion

In the attack on small prey the species behaves like the very primitive spiders, including their relatives of the genus *Sicarius* (Sicariidae) (Levi, 1967), attacking and subduing the prey solely by the use of the chelicerae (Eberhard, 1967).

Large prey is caught by trapping webs and is subdued by biting, but neither holding nor wrapping is involved in the immobilization process. The trapping is a remarkable adaptation to the species' habits, since the web is frequently exposed to prey too large to be captured (e.g., passalid beetles). An extensive capturing web, often destroyed without reward for the spider, would represent a significant loss of energy (through the production of silk).

During the post-immobilization wrapping the spinnerets are applied directly to the prey in a fashion similar to that observed in the diguetids (Eberhard, 1967).

The capturing behavior of *Drymusa dinora* suggests the presence of an effective venom indicating a closer relationship with *Loxosceles*.

The three genera in the family *Scytodidae* share in common the small size of the permanent web and the specialized technique for subduing of prey.

Conclusions

The species should be considered very primitive since no wrapping is involved in the immobilization of prey. There seems to be a tendency for the economy of silk through the reduction of the permanent web and the overcoming of small prey without the use of trap webs.

These behavioral observations, along with the morphological evidence, indicate that it might be best to keep the three genera (*Drymusa, Loxosceles* and *Scytodes*) within one family, the Scytodidae.

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A NEW COCKROACH GENUS (*GURNEYA*) PREVIOUSLY CONFUSED WITH *PINACONOTA* (BLABERIDAE: EPILAMPRINAE).*

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Princis (1967) listed 2 species of *Pinaconota,* viz. *bifasciata* (Saussure) and *obliqua* (Walker). *Ischnoptera* (?) *sicca* Walker was synonymized by Kirby (1904) with *bifasciata,* but I (1973a) showed that Kirby was incorrect in his interpretation of the species and placed *sicca* in the new genus *Alphelixia.* The male genitalia and other morphological characters of *obliqua* indicate that this species is not a *Pinaconota* and a new genus is erected for it (see below).

In describing *Pinaconota,* Saussure (1895) simply stated that the hind metatarsi were very short, with a fringe of long hairs, and a large apical pulvillus. Shelford's (1910) characterization of the genus is as follows: Form depressed. Pronotum trapezoidal, anteriorly and posteriorly sub-truncate, deeply punctate. Scutellum exposed. Tegmina and wings fully developed, extending beyond the apex of the abdomen. Femora moderately spined beneath. Tarsi very short, fimbriate, and entirely unarmed beneath; posterior metatarsus equal in length to the two succeeding joints, its pulvillus large. Arolia very large. In this generic description, Shelford was apparently influenced by his belief that *Ischnoptera* (?) *obliqua* Walker was a *Pinaconota.*

Pinaconota can be recharacterized as follows:

Pinaconota Saussure

Type-species: *Blatta bifasciata* Sauss., Monotypy (1895, p. 337)

Both sexes with tegmina and wings abbreviated, or extending slightly beyond the end of the abdomen. Ventro-anterior margin of front femur with 2 or more, small, heavy spines, followed by a row of small uniformly spaced slender setae, terminating in a large distal spine; ventro-anterior margins of mid and hind femora with 2 or 3 widely spaced spines, with or without distal spines; hind metatarsus short with 2 rows of fine ventral setae; pulvilli and arolia very

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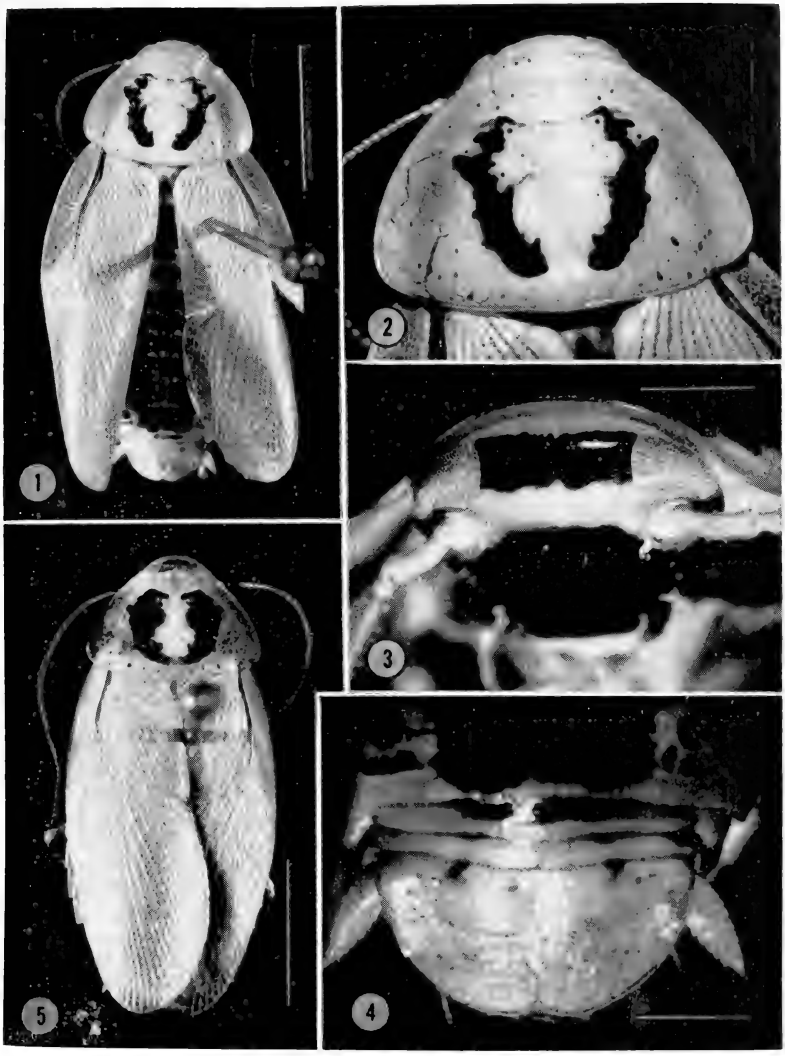


Figs. 1-5. *Pinaconota bifasciata*. 1-4. Male, from Brazil. 2. Pronotum. 3. Head. 4. Terminal abdominal segments (dorsal). 5. Male from S. Cath., Brazil. (scale: figs. 1 and 5 = 5 mm; fig. 2 = 2 mm; figs. 3 and 4 = 1 mm).

large. Supra-anal plate rounded with a mesal indentation. Cerci short, reaching to about the hind margin of supra-anal plate. Subgenital plate (♂) asymmetrical, broadly, but weakly concave on right side; styli about equal. Male genitalia: L2d a small irregularly shaped sclerotized plate separated from L2vm; prepuce densely spicular in part, with or without large spines on the free margin (Figs. 15, 17, 20, 23, 29, 30; see Fig. 29 for naming of parts), a light sclerotized plate present ventral to the L2vm. The membrane lying above the L2vm may have a number of small spines (Fig. 15) but in the flattened KOH preparations are not shown in their normal position (Figs. 20, 23). R2 unique in having a finger-like basal projection directed toward the inner curved margin of the hook (Figs. 16, 18, 21, 31). Right paraproct considerably more developed than the left (Figs. 13, 27-28).

The presence of large spines on the prepuce is, as far as I know, unique for a member of the Epilamprinae, and has only been found in the Blaberinae. However, in that subfamily the spines usually closely surround the L2d (Roth, 1970a). Because of the unusual genital structures, I place *Pinaconota* in the tribe Pinaconotini.

The following is a redescription of *Pinaconota bifasciata* supplementing that of Saussure:

Pinaconota bifasciata (Saussure)
(Figs. 1-23)

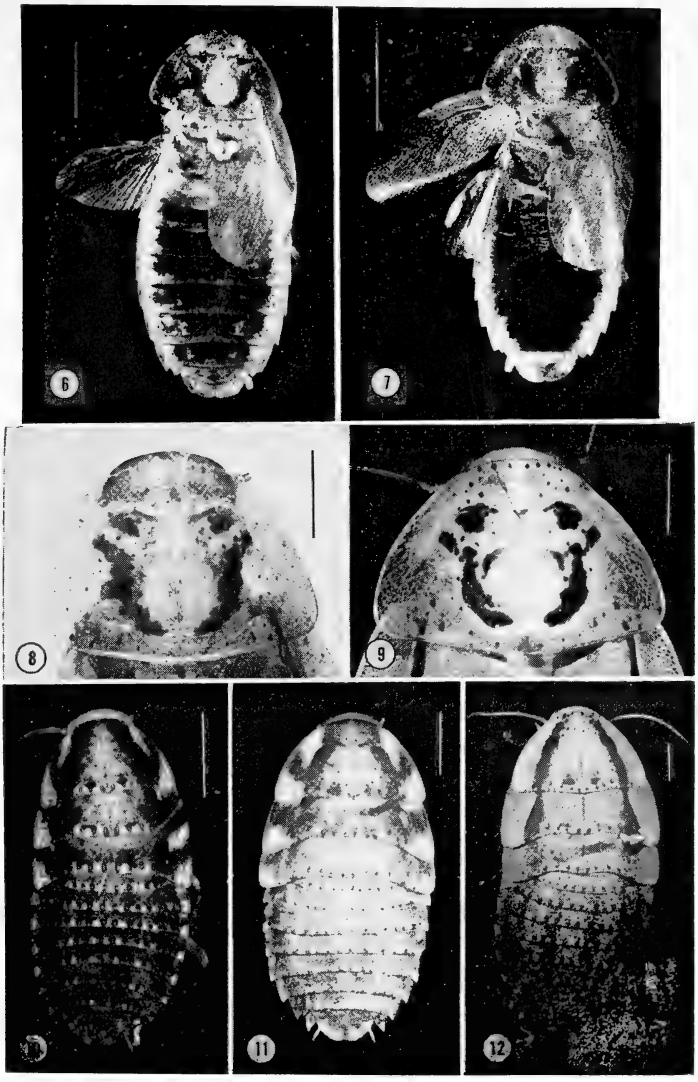
Blatta bifasciata Saussure (Rev. Mag. Zool., 1862, p. 165; Mém. Hist. nat. Mexique, Genève, 1864, 4, p. 98, ♂ ♀).

Phyllodromia bifasciata (Saussure) (Brunner, Nouv. Syst. Blatt. Vienne, 1865, p. 94).

Epilampra bifasciata (Saussure) (Miss. scient. Mexique, Rech. zool. Paris, 1870, pt. 6, p. 84, pl. 2. Figs. 44, 44A).

Pinaconota bifasciata (Saussure) (Rev. suisse Zool. 1895, 3, p. 337).

♂. (Figs. 1, 5, 7). Face smooth with scattered small setae, vertex exposed. Pronotum semi-circular, somewhat flattened but with sides slightly deflexed, hind margin subtruncate or weakly curved. Tegmina abbreviated, reaching to about the middle of fourth tergite (Fig. 7) or fully developed extending beyond the end of the abdomen (Figs. 1, 5), rounded apically; plical furrow strongly arched, the furrows from both tegmina meeting to form a semi-ovoid anal field, anal veins of left tegmen shallowly punctate; veins of right tegmen punctate only in that portion not covered by the overlapping left tegmen; many veins on other parts of the tegmina also shallowly punctate. Abdomen broad. Supra-anal plate rounded, mesally indented. Cerci not extending beyond hind margin of supra-

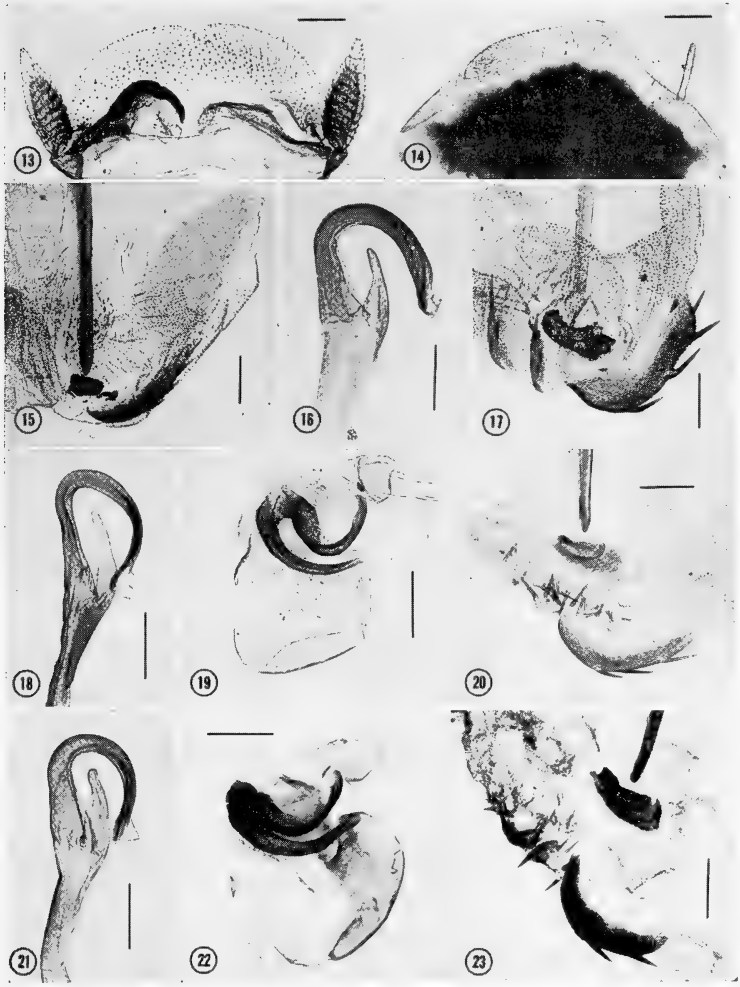


Figs. 6-12. *Pinaconota bifasciatia*. 6. Brachypterous female. 7. Brachypterous male. 8. Pronotum of female shown in fig. 6. (both ♂ and ♀ from Ilha das Alcatrazes, S. Paulo, Brazil.) 9. Pronotum of macropterous ♀ taken at quarantine on a plane in Miami, Florida (with bromeliads), Jan. 20, 1972. 10-12. Three nymphs: 10 and 12. From Brazil, in plane at San Francisco, Nov. 17, 1970 (with bromeliads). 11. From Brazil, at Hoboken, Oct. 30, 1940 (with orchids). (scale: figs. 6-7 = 5 mm; figs. 8-12 = 2 mm).

anal plate (Figs. 4, 13), flattened dorsally with few scattered setae, somewhat convex ventrally covered with many short and a few long setae. Subgenital plate asymmetrical, apex of hind margin subacute, the right side shallowly concave, styli about equal, not extending beyond the apex of the plate (Fig. 14). Leg armament as described for genus: Antero-ventral margin of front femur with 2-6 small but stout spines followed by a row of very small setae. Pulvilli very large, apical on the metatarsi, and covering practically the entire ventral surfaces of the other tarsal segments; arolia very large. Genital phallomeres shown in figures 15-23: L2d an irregularly shaped sclerotized plate separated from L2vm (Figs. 15, 17, 20, 23); preputial membrane modified into a densely spicular area with 3 or more large spines; a pale sclerotized plate continues beyond the dense spicular area (Fig. 15); the membrane above L2vm with many small spines; L1 with a deep, heavily sclerotized, upcurved cleft, the upper lobe smaller than the lower lobe which lacks setae (Figs. 19, 22). R2 strongly curved, the apex partly membranous, enlarged, a large finger-like projection extending from the base toward the inner margin of the curved portion (Figs. 16, 18, 21).

Measurements (mm): Total length, 15-16.5; pronotum length × width, 4.1-4.2 × 5.9-6.2; tegmen length, 12-12.5 (macropterous). 7.6 (brachypterous).

Coloration: Face (Fig. 3) brownish to black, followed by a broad testaceous band just above the antennal sockets, then a broad brownish to black band connecting the tops of the eyes and followed again by testaceous; basal half of clypeus testaceous. Antennae more or less unicolorous throughout, or with basal segments yellowish brown, the remainder darker. Pronotum and tegmina semi-hyaline to subopaque, the less transparent specimens whitish-yellow, the others testaceous. Pronotum with an irregularly shaped, arched, longitudinal, light to dark brownish band on each side of the mid-line, not reaching the borders, but converging posteriorly; surface sprinkled with a few to many brownish dots of variable size (Figs. 1, 2, 5, 7). Humeral vein with a brownish stripe of variable length, the stripe solid (Fig. 5) or pale with dark lines on either side (Fig. 1); right tegmen dark on the portion covered by the left tegmen (Fig. 1). Tergites mostly dark, either solidly dark brown or interspersed with some pale areas, laterally with a broad testaceous or yellowish-white border, sprinkled with small brown dots; in the subopaque ♂ the seventh segment has a round brownish spot on each side (Fig. 4). Sternites dark brown with or without a lateral testaceous border



Figs. 13-23. *Pinaconota bifasciata*. Male structures. 13-14. Supra-anal plate (dorsal) and subgenital plate (ventral; left style missing), respectively. From male taken at Miami (with orchids from Brazil), 26 July, 1971. 15-23. Genital phallomeres: 15-16. L2vm, L2d, and prepuce (15) and R2 (16), from ♂ shown in fig. 5. 17-19. L2d and prepuce (17), R2 (18), and L1 (19) from ♂ shown in fig. 1. 20-21. L2d, and prepuce (20), and R2 (21), from ♂ shown in fig. 7. 22-23. L1 (22), and L2d and prepuce (23), of male whose supra-anal and subgenital plates are shown in figs. 13 and 14. (scale: figs. 13-14 = 0.5 mm; all others = 0.3 mm; all figures from KOH cleared, flattened preparations).

(if present, continuing around the margin of the subgenital plate). Legs testaceous with some brownish areas, especially on front femora.

♀. (Figs. 6, 8, 9). Similar to male except that the subgenital plate is symmetrical and rounded.

Measurements (mm): Total length, 17-21; pronotum length × width, 4.2-5.5 × 6.5-8.2; tegmen length, 14-16 (macropterous), 8.9 (brachypterous).

Nymphs: Nymphs are brownish, and yellowish brown, the markings differing with different instars (Figs. 10-12). Young and older stages have the characteristic head markings of the adult. The pro-, meso-, and metanotum are sprinkled with variable sized raised dots, a row of several elongated ones along the mid-posterior border just above the margin. A similar row of elongated granules along the hind margins of the abdominal tergites, the granules decreasing in size laterally, and smaller on the posterior segments.

Material examined (All specimens from the U.S. National Museum): ♂, ♀ nymph, 2 ♂ nymphs, Brazil (at San Francisco, 17. XI. 1970, with bromeliads); ♀, ♂ nymph, Brazil (at Hoboken, 29, 30. X. 1940, with bromeliads); ♂ and ♀, Corupa (Hansa Humboldt), S. Cath., Brazil, XI. 1944 (♀), XI. 1945 (♂) (A. Maller leg); ♀, Brazil; ♀, Brazil 20. I. 1972 (on plane at Miami, with bromeliads); ♂, Brazil, 26. VII. 1971 (at Miami, with orchids); brachypterous ♂ and ♀, Ilha das Alcatrazes, S. Paulo, Brazil.

I was not able to obtain Saussure's type ♀ but the available macropterous specimens in general fit his description and figure. The pronotal markings of the brachypterous specimens were of a much lighter brown than the long-winged forms and the male preputial modification differed slightly (Fig. 20) from the others (Figs. 17, 23). It is possible that more than one species is represented in the above material but additional specimens, particularly of brachypterous forms are needed before this can be decided.

Walker (1868) described the male of *Panchlora inaequalis* which Kirby (1904) listed under *Tribonium,* and which was placed in *Proscratea* by Princis (1958). The male genitalia of *Panchlora* (Roth, 1971a), *Tribonium* spp. (Roth, 1970)[1], and *Proscratea com-*

[1]The following changes should be made in the explanation of figures in my Zetoborinae paper (Roth, 1970): p. 223, Fig. 18, *Tribonium conspersum* (Guérin) should be *Tribonium spectrum* (Eschtz.); Fig. 19 should be 20; Fig. 20 should be 19 and *Tribonium* sp. should be *Tribonium conspersum* (Guérin); page 234, shown in Fig. 19 should read 20; *Tribonium conspersum* should read *Tribonium spectrum;* p. 235, *Tribonium* sp. should read *Tribonium conspersum* and shown in Fig. 20 should read 19).

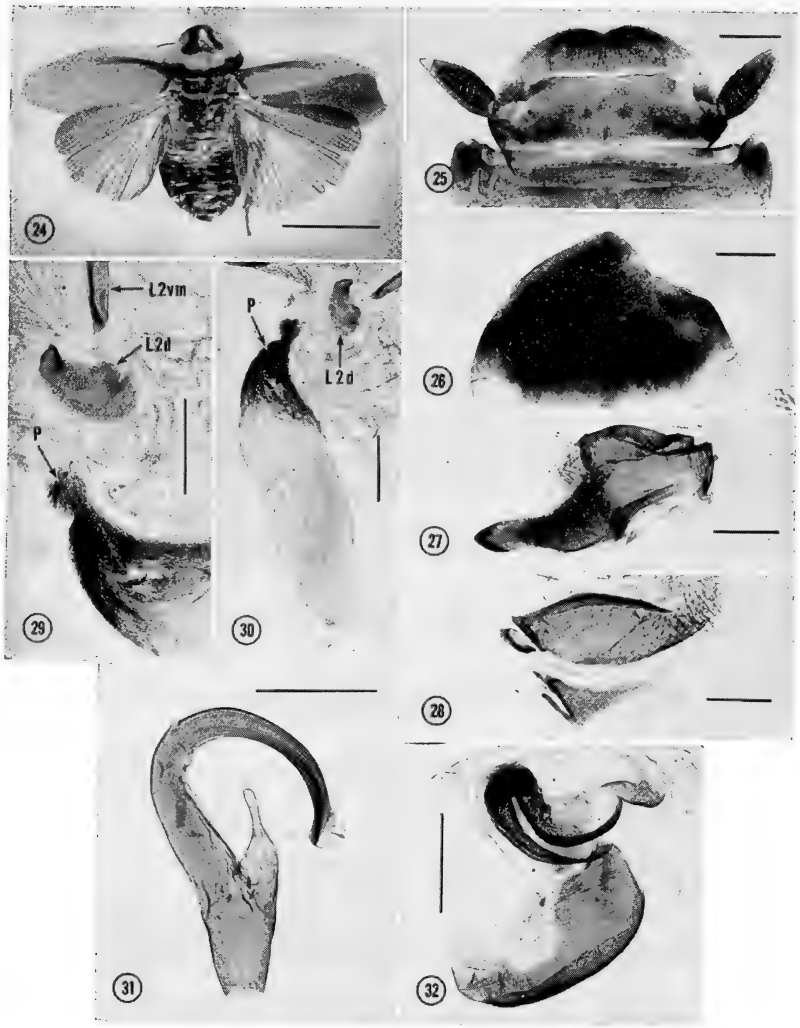
planata (Perty) (Roth, 1973; type of genus, Princis, 1964), are so different from *inaequalis* that it is unwarranted to place this species in any of these genera. The most unusual features of the genitalia of *inaequalis* are the R2 (Fig. 31) with a basal projection extending toward the inner margin of the hook, and the densely setose preputial modification (Figs. 29, 30). The R2, L2d, and L1 (Figs. 29-32) of *inaequalis* are remarkably similar to these structures of *Pinaconota bifasciata* (Figs. 15-23). The prepuce in both have a large faintly sclerotized plate which lies under the L2vm; the prepuce of *inaequalis* differs in lacking some large spines on the border and smaller ones on the membrane above L2vm. Although the color markings and size of *Panchlora inaequalis* differs from *Pinaconota bifasciata* (cf. Figs. 1 and 24), the marked similarity in their genitalia and other characters indicates that the former species should be placed in *Pinaconota.*

The following is a redescription of *Panchlora inaequalis* supplementing that of Walker.

Pinaconota inaequalis (Walker), n. comb.
(Figs. 24-32)

Panchlora inaequalis **Walker (1868, 33, ♂ not ♀ as indicated).**
Tribonium inaequalis **(Walker) (Kirby, 1904, 157).**
Proscratea inaequalis **(Walker) (Princis, 1958, 70, ♂).**

♂ holotype (Fig. 24). Interocular space about twice the width of one eye. Prothorax widest below middle, arched anteriorly, disk flat, slanting laterally; lateral angles rounded, posterior margin slightly convex. Supra-anal plate broadly rounded with a distinct mesal invagination. Cerci reaching to about the hind margin of supra-anal plate (Fig. 25). Subgenital plate asymmetrical, roughly triangular, rounded on the left side and broadly incised on the right; styles absent, but these apparently had been broken off (Fig. 26). Costa of tegmina slightly and regularly curved. Anterior margin of front femur with 5 or 6 heavy spines, more or less uniform in size, followed by about a dozen small uniformly spaced piliform setae, terminating in a large distal spine (Type B); posterior margin with 1 stout spine about ¼ distance from apex; distal spine present; genicular spine absent; anterior margins of mid and hind femora with 2 or 3, and posterior margins with 3 widely spaced, small stout spines; genicular spines present as well as distal spines



Figs. 24-32. Adult ♂ of *Pinaconota inaequalis* (Walker) (holotype of *Panchlora inaequalis* Walker). 24. Adult. All structures shown in the following figs. are from this ♂. 25. Supra-anal plate and cerci (dorsal). 26. Subgenital plate (ventral). 27. Right paraproct. 28. Left paraproct. 29-32. Parts of the genitalia; fig. 30 shows the entire preputial modification, which is only partly shown in fig. 29. (L2vm = ventromedial sclerite (only apex is shown); L2d = dorsal sclerite of second left phallomere; P = preputial membrane). 31. R2 (second sclerite of right phallomere). 32. L1 (first sclerite of left phallomere). (scale: fig. 24 = 10 mm; figs. 25-26 = 1 mm; figs. 27, 28, and 32 = 0.5 mm; fig. 29 = 0.4 mm; figs. 25-32 from KOH cleared, flattened preparations on 2 slides labeled 66 BMNH).

on both margins of mid and hind femora.[2] Tarsal claws equal, arolia and pulvilli well developed. Right and left paraprocts shown in figures 27 and 28. Genitalia as shown in figures 29-32; L2d is a flat unevenly sclerotized plate separated from L2vm (Figs. 29-30); prepuce highly modified with an area of densely packed small setae leading into a large smooth, banana-shaped (when flattened) sclerotized plate (Fig. 30). R2 with an elongated process extending upward toward the curved inner margin of the hook (Fig. 31); L1 with a curved, heavily sclerotized cleft, lower lobe lacking setae, with an unevenly broad, sclerotized marginal area (Fig. 32).

Measurements (mm): Overall length about 21; length and width of pronotum, 5.6 × 8.6.

Coloration: Head black. Pronotum brownish yellow, semi-hyaline; a broad black inverted Y-shaped band extends from the anterior arched border to the disk; a broad black, undulating band extends along the posterior border between the two lateral angles. Abdominal tergites and sternites piceous. Tegmina reddish tawny, costal area testaceous and corciaceous towards base, with a dark humeral line; right tegmen with a large blackish region where it is covered by the left tegmen. Wings brownish.

Material examined: Holotype ♂ of *Panchlora inaequalis* Walker, locality unknown. From Mr. Argent's Collection. Type in British Museum (Natural History).

Shelford (1907) stated that *Ischnoptera* (?) *obliqua* Walker "appears to be undoubtedly referable to the genus *Pinaconota,* Sauss.; it can be distinguished from the only other species in the genus *P. bifasciata,* Sauss., by its much larger size." *P. obliqua* differs markedly from *bifasciata* in femoral armature, relative length of cerci, bulging eyes, and ♂ genital phallomeres. Because of the morphological differences, especially in the 3 genital phallomeres, I am placing *obliqua* in a new genus characterized as follows:

Gurneya n. gen.[3]

Type-species: *Ischnoptera* (?) *obliqua* Walker (1869, p. 148) (present designation).

[2]Princis (1958) placed *inaequalis* in *Proscratea.* The femoral armament of a female of *Proscratea complanata* was as follows: Anterior and posterior margins of front femur unarmed except for 1 distal spine on each; genicular spine absent. Both margins of mid femur unarmed; distal spines lacking; genicular spine present. Anterior margin of hind femur unarmed; hind margin with 3 widely spaced heavy spines; distal spines absent, genicular spine present.

[3]The genus is named in honor of Dr. Ashley Gurney, orthopterist at the United States National Museum, who has helped me considerably in my taxonomic studies of the Blattaria.

♂. Vertex, face, and pronotum deeply punctate (Figs. 34-35). Entire ventro-anterior margin of fore femur armed with a row of small, bimarginally serrated, closely spaced spines, lacking a large distal spine (Fig. 36); ventro-anterior margin of mid femur similarly armed but the spines fewer and not uniformly spaced. Tarsi very short, fimbriate, unarmed beneath. Supra-anal plate rounded, entire. Cerci long, extending well beyond hind margin of supra-anal plate (Fig. 38). Subgenital plate asymmetrical, with a broad shallow incision on right side (Fig. 39). Styles equal, not extending beyond hind margin of subgenital plate (Fig. 39). Genital phallomeres; L2d absent, prepuce spiculate, otherwise unmodified (Fig. 40). R2 with a deep subapical incision which extends to about the middle of the hook (Fig. 41); L1 with the upper lobe (above the cleft) elongate and more narrow than the lower (Fig. 42).

In *obliqua,* the absence of an L2d and shape of the spicular surface of the prepuce (though lacking some long "silky" hairs on one side) resembles the same structure in *Alphelixia* (see Figs. 21 and 23, *in* Roth, 1973a). The hooked phallomere (R2) resembles this structure in certain genera of Epilamprinae (e.g. *Litopeltis,* see Fig. 37, *in* Roth, 1971) and Blaberinae (e.g. *Blaptica,* see Fig. 57, *in* Roth, 1970a). The shape and sclerotization of the L1 differs from that found in the other genera with similar appearing R2's.

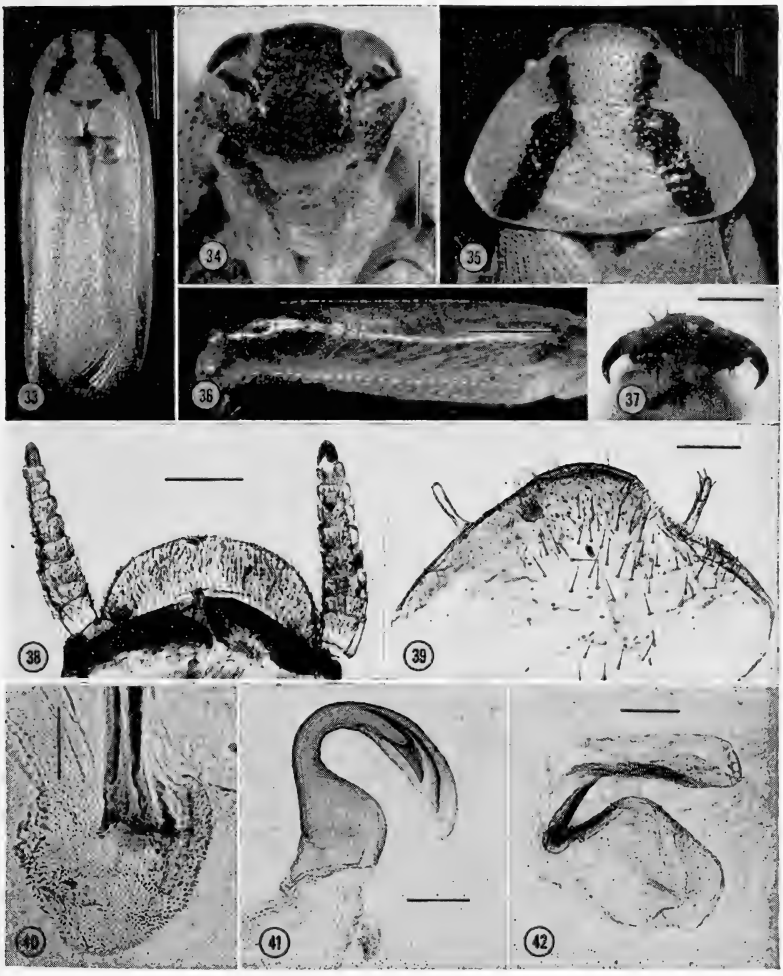
Gurneya obliqua (Walker), n. comb.

(Figs. 33-42)

Ischnoptera (?) *obliqua* Walker (1869, 148, ♂).

Pinaconota obliqua (Walker) (Shelford, 1907, p. 496, ♂).

♂. (Fig. 33). Vertex and face (Fig. 34) deeply punctate, clypeus nearly smooth. Eyes large, bulging, their upper margins raised above the margin of the vertex, wide apart, the distance between them only slightly less than the distance between the antennal sockets (Fig. 34). Pronotum with scattered deep punctures, transversely elliptical, anterior margin almost straight, not covering vertex of head, posterior margin nearly straight, sides deflexed (Fig. 35). Tegmina with basal fourth punctate, covering the abdomen. Scutellum exposed, punctate. Supra-anal plate entire, rounded, its surface and hind margin covered with small fine setae; cerci more than twice the length of supra-anal plate (Fig. 38). Subgenital plate slightly asymmetrical, the right side weakly indented; styli about equal, short, not extending beyond hind margin of subgenital plate (Fig. 39). Legs short, front and mid tibiae shorter than their corresponding femora. Front femur: entire ventro-anterior margin armed with about 30 small, bimargin-



Figs. 33-42. *Gurneya obliqua* (Walker). Holotype ♂ of *Ischnoptera* (?) *obliqua* Walker. All structures shown in figs. 34-42 are from the type. 33. Adult. 34. Head (frontal view). 35. Pronotum. 36. Front femur (anterior surface). 37. Tarsal claws and arolium of prothoracic leg (end view). 38. Supra-anal plate and cerci; the dark structures are paraprocts seen through the cleared tergite (dorsal). 39. Subgenital plate (ventral). 40-42. Genital phallomeres: 40. Apex of L2vm, and preputial membrane. 41. R2. 42. L1. (Specimens shown in figs. 38-42 are KOH treated, cleared, flattened preparations on a slide); (scale: fig. 33 = 5 mm; figs. 34-35 = 1 mm; figs. 36, 38-39 = 0.5 mm; fig. 37 = 0.25 mm; fig. 40 = 0.1 mm; figs. 41-42 = 0.2 mm).

ally serrated, close-set row of spines (Fig. 36); enlarged distal spine absent; posterior margin with 5 larger bimarginally serrated spines, 2 of them relatively close together basally, the others much wider apart; distal spine present; genicular spine absent. Mid femur: entire ventro-anterior margin with about 13 bimarginally serrated spines, those on the distal third somewhat closer together than the others; distal spine obsent; posterior margin with 5 spines plus a small distal spine; genicular spine present. Hind femur: anterior ventral margin with 7 spines; enlarged distal spine absent; ventral posterior margin with 3 or 4 larger spines; distal spine absent; minute genicular spine present. Tarsi short, unarmed beneath, both tibiae and tarsi fimbriated; all metatarsi shorter than the remaining segments combined, of their respective tarsi. Tarsal claws simple, about equal or one slightly smaller (possibly broken or worn) than the other; arolia large, roughly triangular in end view (Fig. 37); pulvilli very large and, except for those on the metatarsi, cover the entire ventral surface of the segments. Genitalia shown in figures 40-42. L1 with a deep sclerotized cleft; the upper lobe (above cleft) elongate, relatively narrow, roughly rectangular extending slightly beyond margin of lower lobe; lower lobe much larger than upper, and without setae (Fig. 42). L2d absent, preputial membrane spicular, unmodified (Fig. 40). R2 broadened at base, a deep subapical incision extends to about the middle of the hook (Fig. 41).

Measurements (mm): Overall length, 21; body length, 18; tegmen length, 17; pronotum length × width, 3.9 × 6.2.

Coloration: Pale testaceous. Head castaneous, fuscous band between eyes; clypeus, mouthparts and antennae testaceous. Two angulate black stripes on the pronotum extend from anterior to posterior margins; anteriorly the stripes are narrow and converge; posteriorly the stripes are broader and diverge (Fig. 35). Tegmina with a short humeral castaneous stripe. Scutellum marked with castaneous. Abdomen and legs pale testaceous.

♀. Unknown.

Material examined: Holotype ♂ of *Ischnoptera* (?) *obliqua* Walker. Brazil. Type in Hope Department of Entomology, Oxford Museum, England.

Summary

The genus *Pinaconota* is redescribed together with 2 species, *P. bifasciata* (Sauss.) and *P. inaequalis* (Walker). A new genus *Gurneya* is erected for *Ischnoptera* (?) *obliqua* Walker which Shelford had incorrectly assigned to *Pinaconota*.

Acknowledgements

I thank Dr. David Ragge, British Museum (Natural History), London for the loan of the type of *Panchlora inaequalis* Walker, Dr. M. W. R. de V. Graham, Hope Department of Entomology, Oxford, for the loan of the type of *Ischnoptera* (?) *obliqua* Walker, Dr. Ashley Gurney, U.S. National Museum for specimens of *Pinaconota bifasciata* (Saussure), and Mr. Samuel Cohen for taking the photographs.

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MEROPE TUBER (MECOPTERA): A WING-BODY INTERLOCKING MECHANISM

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As an insect pushes its dorsal surface against obstacles while moving through a substrate, the wings will tend to be forced apart. In many Coleoptera, such divergence is prevented by a complex of devices interlocking the elytra with the thorax and abdomen. A common interlocking mechanism involves intermeshing of parallel arrays of setae angled towards the potentially disrupting force (Fig. 2). A similar high friction binding system on the mesojugum and metascutellum of *Merope tuber* provides additional evidence for the ground dwelling habits of this rare mecopteran.

The fore-jugal lobe of *Merope* is highly modified relative to its counterpart on the hind wing and as compared with the jugal regions of other panorpoids (Fig. 1; JL2, JL3). It does not bear setae and does not appear to function in wing coupling. More importantly, the mesojugal lobe is much thicker, more heavily sclerotized than the wing proper, is quite rigid, yet capable of slight movement about the third anal vein, but does not fold over as the wing comes to rest. The ventral surface is completely covered with uniformly small (.007 × .003 mm) flat topped carinae, angled posteriorly and organized in rows perpendicular to the long axis of the wing (Figs. 1, JL2; 3, 4). The metascutellum bears two patches of anteriorly projecting ridges about twice as long (.017 × .003 mm) but about as high as those on the fore wing (Figs. 1, R, S3; 5).

In rest position, the jugal lobes lie close together and directly above the striate metathoracic areas. When so placed, a small ventral movement will cause the slanting nearly parallel ridges to intermesh. Two functions, which may be combined, may be served by the juxtraposition of parallel carinae: stridulation and interlocking. Stridulation is an unlikely function for these structures. As the wing moves medially to rest, the ridges move parallel to one another, not

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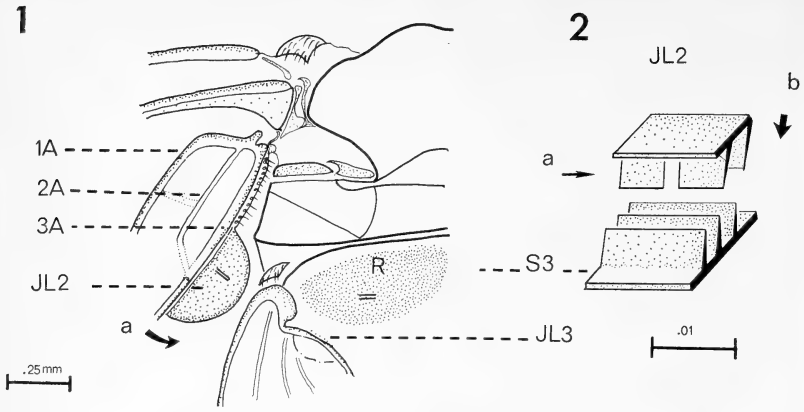
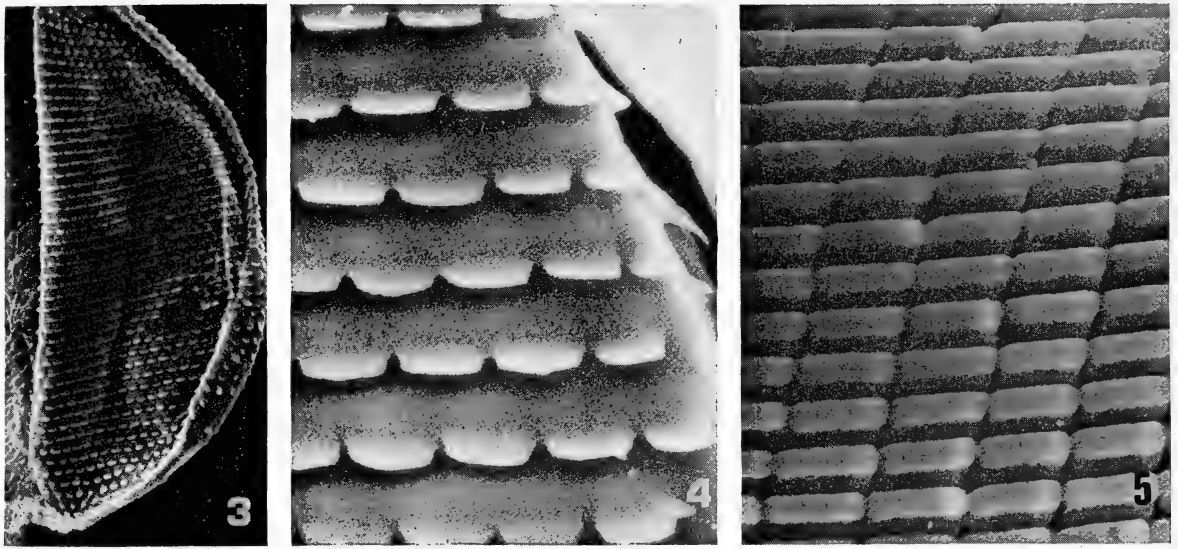


Figs. 1-2. Wing-body interlocking mechanism of *Merope*. Fig. 1. Left half of pterothorax, dorsal view. As the fore-wing moves medially (a); parallel ridges, indicated by two heavy lines, on the jugal lobe (JL2), and on the metascutellum (R, S3) are brought into contact. Fig. 2. Model of interlocking system, posterior view. Small arrow (a) indicates direction of emplacement as wing comes to rest, see Fig. 1; large arrow (b) the direction of intermeshing of the slanted ridges. 1A, 2A, 3A, anal veins; JL2, JL3, meso- and metajugal lobes; R, ridge bearing patch of metascutellum, S3; a, direction of wing movement; b, direction of interdigitation.

perpendicularly as in many sound producing structures (Fig. 2, a). Stridulatory mechanisms are not known in Mecoptera (Riek 1967). The geometry of ridge interdigitation, however, is precisely that required to resist postero-lateral wing displacement during locomotion within a substrate or interstitial spaces. The unique jugal lobe and metascutellar structures of *Merope* may serve then as a wing-body interlocking mechanism which increases structural integrity during crawling within a matrix.

Other structural features and meagre biological data suggest that *Merope* is a substrate inhabitant not a surface dweller as are other winged Mecoptera. The body is dorso-ventrally flattened; the pleural axes of the undifferentiated thoracic segments are sharply inclined from the vertical (Mickoleit 1967). The fore wing is somewhat tegmenized, being thicker and more heavily sclerotized than the hind wing. Antennae and legs are short; pterothoracic appendages may operate almost entirely within the outlines of the flattened wings. Little membrane is exposed between tagmata and between abdominal segments. These characters result in greatly reduced cross section area



Figs. 3-5. Wing-body interlocking mechanism of *Merope*. Scanning electron micrographs. Fig. 3. Mesojugal lobe, ventral view, magnification ca. 40×. Fig. 4. Detail of jugal lobe, ca. 1.3K. Fig.. 5. Detail of ridge bearing zone of metascutellum, ca. .65K.

during locomotion and improved structural integrity relative to other panorpoids. Some specimens have been taken under logs or stones, as were the only known examples of *Austromerope*. The photographs in the original description (Killington 1933) show that the jugal lobe of this Australian form is similar to that of *Merope* in size and shape. Several lines of evidence point towards a marked divergence of meropeids from surface dwelling, loosely constructed configurations of related taxa.

The transformations required to derive *Merope* from a generalized mecopteran are parallel and analogous to those hypothesized for the very early evolution of substrate dwelling Coleoptera (Hlavac 1972). The ability to keep flexible wings in place under stress through interlocking devices is an obvious precursor for the development of elytra. Meropeids may then represent an attempt, albeit a feeble one, by another holometabolous lineage to occupy the substrate adaptive zone.

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THE UNUSUAL WEB OF *SPILASMA TUBULOFACIENS*, WITH TAXONOMIC NOTES ON THE SPECIES (ARANEAE: ARANEIDAE)*

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During December 1972 I had the opportunity to visit French Guiana to study some of its little known amblypygid fauna. While searching for amblypygids I came across the unusual web of an araneid, *Spilasma tubulofaciens,* and was able to make some observations in the field.

I would like to acknowledge the gracious help and encouragement given by Dr. Herbert W. Levi, who also provided the laboratory facilities to complete this work. I would like also to thank Dr. J. J. de Granville for his hospitality and guidance in Cayenne, for the use of ORSTOM facilities in Saül, and for many other favors.

Web of *Spilasma tubulofaciens*

Figures 6-7

Spilasma tubulofaciens females were found in a forest patch clearing occupied with mixed growth of shrubs (mainly Rubiaceae and Leguminoseae), 2-3 m from the muddy banks of Crique Limonade, French Guiana. The suspension lines of the web were attached between leaves of a rubiaceous shrub, about 1.2-1.4 m from the ground. In the middle they inserted at the apex of the conical retreat. The snare region was below, hanging obliquely, and had 16 radii and more than 28 turns, with no distinct frame threads. It showed numerous torn spaces and repairs, giving a general appearance of long use and disorganization. No major changes were introduced by the spiders during the night before they were collected next morning. The suspension lines were quite taut, forming nearly a straight horizontal line (Fig. 6). The outer surface of the conical retreat was rough, made up of diverse materials, predominantly remains of insect prey (small coleoptera, flies, etc.) and vegetable matter (protonema of mosses, small bark fragments, vegetable debris). This debris was firmly fixed to the surface by underlying, fine threads of silk. The inside of the retreat was smooth, lined with silk. The

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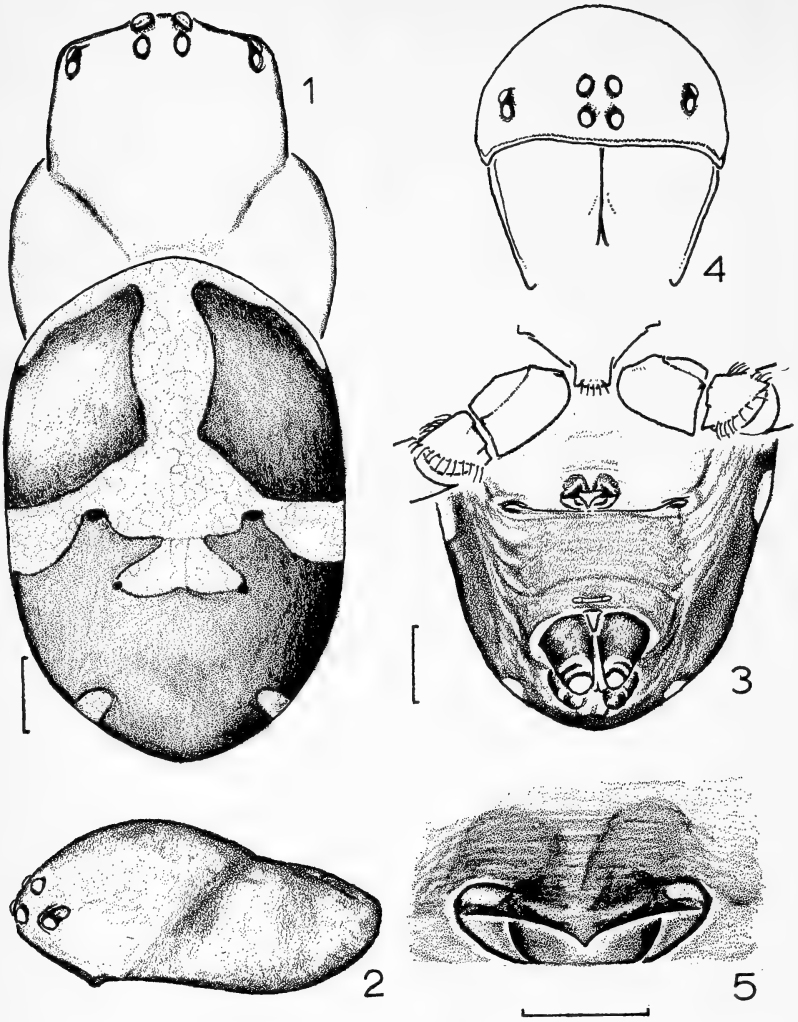

Figs. 1-5. *Spilasma tubulofaciens* (Hingston), female. 1. Dorsal view, appendages not represented. 2. Lateral view of carapace. 3. Ventral view of abdomen. 4. Head and part of chelicerae from in front. 5. Epigynum. Size indicators: Figs. 1-4, 0.5 mm. Fig. 5, 0.2 mm.

Fig. 6. *S. tubulofaciens* (Hingston), frontal view of web and retreat (entrance of retreat closed), drawn from photographs. Suspension lines shaded.
Size indicator: 10 mm.

broad, lower end of the retreat had a transverse, single opening with two lips, the posterior lip being the longer. The lining of the anterior lip appeared thinner and more flexible. The supporting lines were strong, reinforced with silk, and contained numerous moss fragments, particularly close to the insertion on the retreat. There were also remains of insects and vegetable matter. The spider remains inside the retreat, and waits head down for its prey, a characteristic position of the orb-weaving spiders. When I offered living ants, which I placed on the lower corner of the catching web, the female dashed out of the retreat rapidly, wrapped its prey (Fig. 9), bit it, and promptly returned to the retreat, without eating the prey.

Discussion. By changing the position of the hub (coincident in this case with the retreat) to a peripheral, uppermost position, an additional load of tension has been placed on the suspension lines. Additional tension has also been brought to these lines by the taut, almost straight line, to which they have been drawn. Consequently the spider has carefully reinforced the lines with extra layers of silk, enclosing different building materials, and they no longer function in prey capture but to support the rest of the web and the retreat. It differs from *S. artifex* Simon, which Simon, in 1896, described as hanging the retreat and catching web from a single perpendicular

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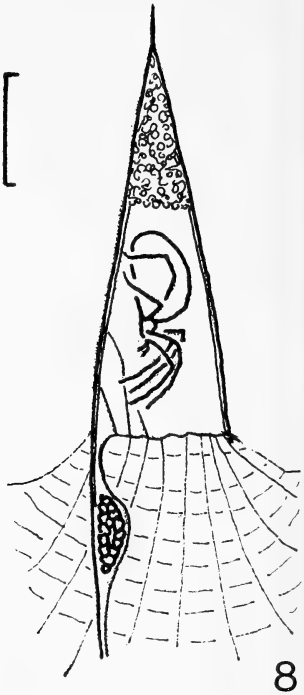

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Fig. 7. *S. tubulofaciens* (Hingston), closer frontal view of the retreat, open. Posterior lip not shaded.

Fig. 8. *S. artifex* Simon, schematic representation of a cross section of the retreat. Posterior lip of the retreat hangs loose, enclosing mass of eggs (Modified from Simon, 1896, pl. 12, fig. 4).

Size indicators: Figs. 7-8, 5 mm.

suspension line (Fig. 8) and having a catching web parallel to the floor, with an empty segment.

The numerous repairs in the web of *S. tubulofaciens,* the thickness of the suspension lines, and the elaborate construction of the retreat all suggest that this web is long lasting (relative to the life span of the spider), and with time is repaired and modified. The retreat of the younger female had more space for occupancy than the retreat of the older female (as determined by body length as a percent of the length of the retreat), the space perhaps serves to accommodate additional growth of the spider without having to enlarge the retreat. Additional collections might verify this observation.

Nielsen (1928, pp. 534-535) has excellent photographs of *Achaearanea saxatile* (Koch), a theridiid, building a similar type of conical retreat on the ground and later scaffolding it to the desired height. It is likely that a similar (energy saving?) strategy is used by *S. tubulofaciens,* instead of making numerous trips to carry and assemble the materials above the ground, although above the ground modifications and repairs might be introduced at a later date.

The adaptive convergence of webs has been discussed recently by several authors (see Kullmann, 1972). Strangely, emphasis in their discussions has been placed on considering orb webs as indivisible entities which appear to have evolved as a unit. Although interactions must likely occur among the major structural components of the web (hub, retreat, and capture threads — snare), my impression is that each has distinct adaptations to cope with in response to environmental and physiological cues (e.g. the retreat to best hide the spider). The selective forces which might bring about evolutionary changes in these components, by selecting particular motor patterns of the spider, must differ and thus these components have evolved as distinct characters, although not totally independent.

Taxonomic notes

Spilasma tubulofaciens (Hingston), comb. nov.

Figures 1-5

Epeira tubulofaciens Hingston, 1932, A naturalist in the Guiana Forest, E. Arnold & Co., p. 366. From Guyana, Essequibo River. Web illustrations, pp. 150-153; no type material left.

Araneus tubulifaciens, Bonnet (1955, Bibliographia Araneorum, 2: 620, 80), makes emendation of specific name which is of Latin derivation.

Records. 2 ♀♀ (one immature) from French Guiana, Crique Limonade, 3-4 km S. of Saül, 21-22.VIII.1972. Adult ♀ and retreats deposited in the MCZ, Harvard collection.

In his 1932 work, Hingston described 27 new species from eight different genera collected during an expedition to Guyana in 1929. Hingston left no type material for his new species and his descriptions were very general, lacking diagnostic characters (Levi, 1963, p. 493). Nevertheless, Hingston included descriptions and detailed sketches of the webs of his new species, which may help to validate some of his names, in some instances. Lehtinen (1967, p. 201) considered that the only way to treat the species described by this author would be to propose all of them as "nomina dubia." I am convinced that the specimens which I have collected belong to one species described by Hingston as *E. tubulofaciens*. I base my assertion mainly on the unique abdominal and leg coloration patterns, and the remarkable architecture of the retreat and the catching web, which matches Hingston's descriptions. Although there is the possibility of sibling species, I have decided for the sake of stability in nomenclature to retain Hingston's name.

Description. Carapace, chelicerae (except claws), pedipalps, and dorsal surface of legs brownish yellow, with the two posterior legs a darker brown. Inner margin of endites white. Sternum and labium reddish brown. Carapace covered with fine-pointed bristles which become longer toward the anterior margin. Carapace with a well-defined cephalic suture. Ventral coloration of the two first legs is reddish orange but this pigmentation washed away after preserving the specimens in alcohol. Abdomen is longer than wide and slightly wider in its anterior half. Dorsum of abdomen with a broad, white H-shaped mark over black background, positioned transversely on the anterior half. Near its middle, the posterior bar of the H mark has an additional smaller triangular white mark pointing anteriorly and two dorsal black sclerites. On its posterior third, latero-ventrally, two elongated white marks occur, one on each side of the abdomen. Venter with a light colored epigastrium and colulus. Anterior median eyes are largest and closely positioned, 0.7 diameter apart. Posterior medians one diameter apart. Laterals closely set on a common raised black-pigmented carapace projection. Total length 4.9 mm. Carapace 2.6 mm long, 2.3 mm wide. First femur, 2.1 mm; patella and tibia, 2.0 mm; metatarsus, 1.1 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.3 mm; fourth, 1.7 mm.

Diagnosis. Spilasma males are not known. Females of *S. tubulofaciens* have distinct body coloration and web construction, different from the only other South American species: *S. tridecimguttata* Simon 1896 from the Amazonas and *S. artifex* Simon 1896 from San Esteban, Venezuela. A third species, *S. africana* Simon 1903,

Fig. 9. Female of *S. tubulofaciens* wrapping prey on web.

is only known from Equatorial Guinea. Hingston (1932, p. 366) described a species, *E. sacculifaciens,* with similar conical retreat and web architecture to *S. tubulofaciens,* which, I suspect, will eventually be ascribed to the genus *Spilasma* when new material is collected. Its reported size, 1.5 mm, suggests it might be an immature specimen as the other known species of *Spilasma* range from 3 to 6 mm in length.

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WING-FOLDING IN THE PALEOZOIC INSECT ORDER DIAPHANOPTERODEA (PALEOPTERA), WITH A DESCRIPTION OF NEW REPRESENTATIVES OF THE FAMILY ELMOIDAE

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The order Diaphanopterodea is closely related to two other Paleozoic paleopterous orders, the Palaeodictyoptera and the Megasecoptera, all three having elongate, haustellate mouth-parts. In the history of the study of paleopterous insects, the Diaphanopterodea represent the most intriguing group. The order combines the basic characteristics of the Paleoptera, fluted wings and very long, multisegmented cerci, with the ability to fold the wings backwards over the abdomen, which is the principal character of the Neoptera. Since that resting position of the wings indicates a major development in the evolution of insects, as well as major achievement in adaptation to more varied environment, its occurrence within the Paleoptera is of great interest.

At present there is general agreement among students of insect evolution that wing-folding ability arose at least twice in insects — in the Neoptera and in the Diaphanopterodea among the Paleoptera (Rohdendorf 1962, Carpenter 1963, Sharov 1971). It has been assumed that the wing-folding mechanism in the Diaphanopterodea was probably different from that in the Neoptera, but the structure of the axillary region of the diaphanopteran wing has not actually been known. While examining all known specimens of Diaphanopterodea from the Lower Permian deposits of Czechoslovakia, Kansas and Oklahoma, I succeeded in finding a dozen wings, belonging to the families Elmoidae, Martynoviidae and Asthenohymenidae, with the bases of the wings at least partially preserved. The present paper is concerned only with the family Elmoidae; the two remaining

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families and the wing base morphology of the Palaeodictyoptera and Megasecoptera will be discussed elsewhere.

The new material includes six new genera and ten new species of Elmoidae from the Lower Permian beds near Obora in Moravia, Czechoslovakia. The base of the wing is well preserved in one specimen only, *Permodiapha carpenteri* n.sp. (No. 8/1974), and incompletely preserved in seven other specimens.

Since no definitive studies of the wing bases of the extant Paleoptera [Odonata and Ephemeroptera] have been made, some difference of opinion exists about the interpretation of the basal sclerites. The interpretation of the diaphanopteran structures used in this paper should be considered only as tentative. The terminology employed is derived from the account of the wing base of Odonata by Tannert (1958), since the fore wing base in the Ephemeroptera has never been described in functional terms. For further comparison, the wing base structures of the related family Martynoviidae (undescribed material) and the related order Palaeodictyoptera (Kukalová 1960, 1969, 1970) have been used.

Family Elmoidae

Elmoidae Tillyard 1937: 82; Carpenter 1943: 56; Carpenter 1947: 27; Rohdendorf 1962: 69; Carpenter 1963: 249.
Parelmoidae Rohdendorf 1962: 71.

The family Elmoidae was originally assigned by Tillyard to the paleopterous order Megasecoptera because of the similarity in the venation pattern. This point of view was followed by Carpenter in his emendation of Elmoidae in 1943 and 1947, although he subsequently (1954) separated the Elmoidae, along with the Diaphanopteridae and related families, into a distinct suborder (Paramegasecoptera), on the basis of the folded, resting position of the wings. Later, Rohdendorf (1962) and Carpenter (1963) independently reached the conclusion that these families had to be referred to the separate order Diaphanopterodea, established by Handlirsch (1919). A detailed evaluation of the phylogenetic position of Elmoidae and Diaphanopteridae within the order, and of Diaphanopterodea within the Paleoptera has been given by Carpenter (1963).

Until now, the family has been known by only three genera, all from the Lower Permian of Kansas and Oklahoma — *Elmoa, Parelmoa,* and *Pseudelmoa,* represented by five species. The new fossils from Moravia contribute additional and varied morphological features, which broaden the family characteristics formerly used. In the Moravian material thickened cuticular spots are sometimes pres-

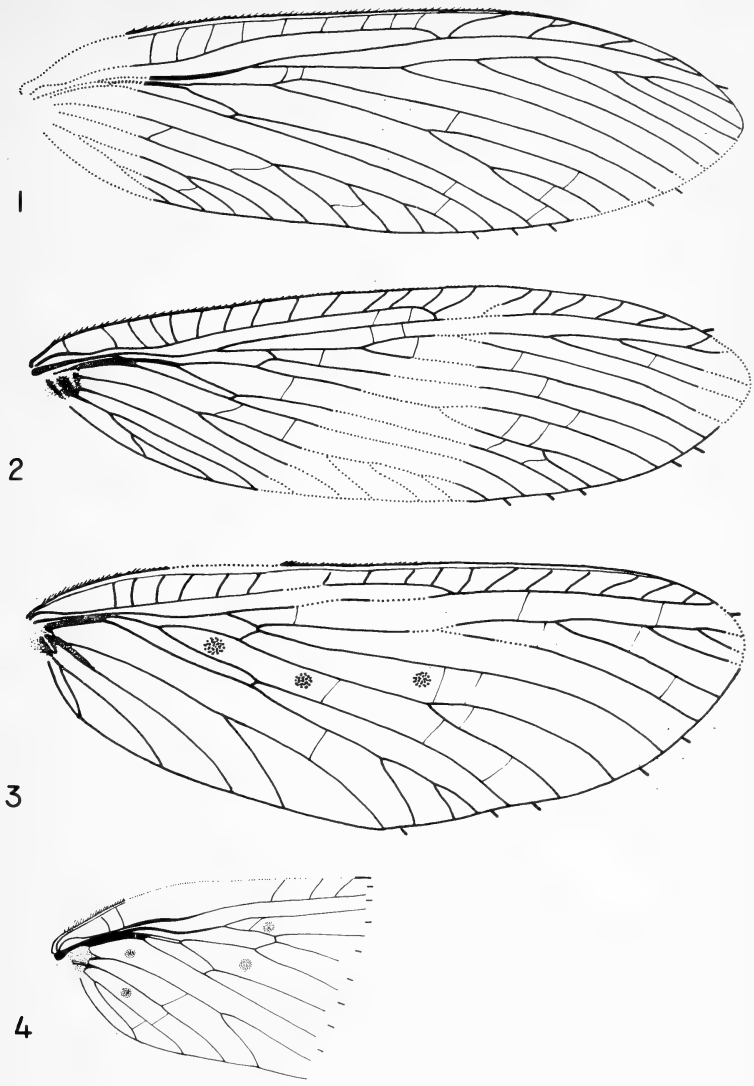
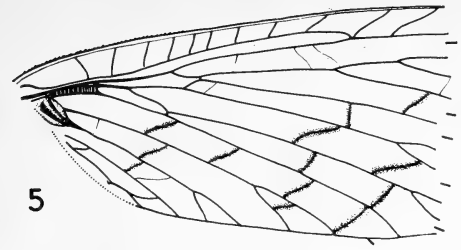
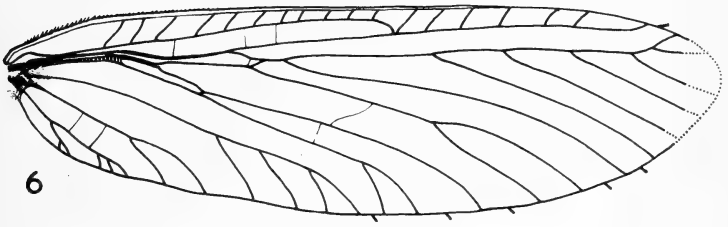


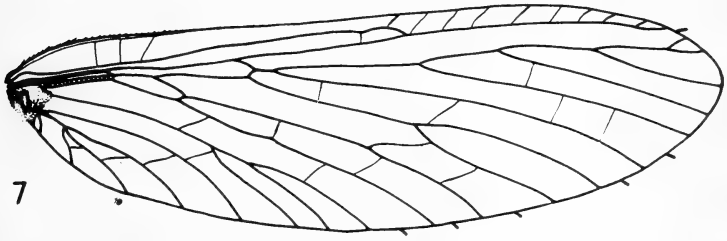
Fig. 1. *Elmodiapha ovata* n.sp., specimen 1/1974, fore wing. Holotype. Fig. 2. *Elmodiapha ovata* n.sp., specimen 2/1974, fore wing. Fig. 3. *Protodiapha maculifera* n.sp., specimen 3/1974, hind wing. Holotype. Fig. 4. *Protodiapha maculifera* n.sp., specimen 4/1974, hind wing.

ent on the wings, between the veins, and the main veins are covered with a series of setae. Costa is flattened and in larger wings sometimes serrated; it often carries a series of long setae, which are more pronounced basally. Subcosta consistently forms a conspicuous bend at the very base, probably related to the wing-folding process. Radius is always fused basally with the stem of the media. M, after diverging from R, immediately coalesces or joins either the stem of Cu and CuA, or directly CuA, for a short distance. MA and Rs are connected in North American Elmoidae by a cross vein. In Moravian Elmoidae the cross vein is present in only three species. In others, MA almost touches Rs or MA joins Rs at a point, or for a short distance, or both veins are anastomosed for a short distance. Cubitus runs closely to, or touches, R. The stem of Cu is always ribbon-like, deeply concave, broad and flattened. CuA and CuP originate near the point at which M diverges from the common R + M stem. Soon after diverging from M, CuA approaches CuP and is connected with it by an oblique cross vein. This feature seems to be a stable character of the family. Anal veins start from the posterior part of the sclerotized region, which is the thickened part of the wing membrane posteriorly from Cu and distally from the basal fold (fig. 10,S). It undoubtedly served as a reinforcement of the wing base while folding the wings backwards. The basal plate is represented either by the enlarged cubitoanal plate, or by the fusion of the median, cubital, and anal plates. It is partly homologous with the fused subcostoanal plate of the Palaeodictyoptera, the fused basal plate of the Ephemeroptera, and the radioanal plate of the Odonata. The basal fold runs between Sc and R + M, crosses R + M where it is flattened and weakly sclerotized, follows closely the distal margin of the fused basal plate, and crosses the anal part of the sclerotized region (fig. 10,B). The axillary sclerite articulates with the proximal margin of the basal plate and with R. Its size and shape are not known.

The family Elmoidae, as long as it was known only by North American species, was well separated from the related Upper Carboniferous family Diaphanopteridae. The family Diaphanopteridae, represented by *Diaphanoptera* (France) and *Philiasptilon* (Soviet Union, Kuznetsk Basin), was characterized by the presence of the anastomosis between MA and Rs. In the Permian material from Moravia, however, this feature is highly variable. In *Elmodiapha* and *Protodiapha* (new genera), MA and Rs are connected only by a cross vein, as in the Elmoidae from Kansas and Oklahoma. In the other Moravian genera, MA and Rs are either touching each other







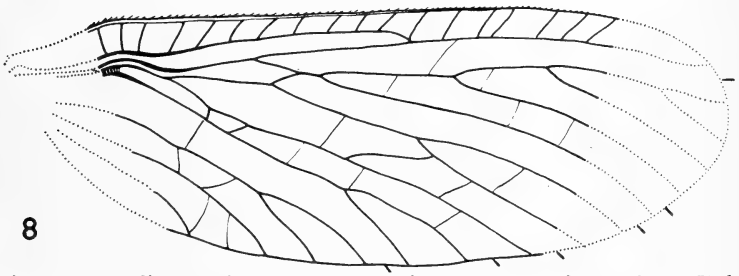


Fig. 5. *Protodiapha lineata* n.sp., specimen 5/1974, fore wing. Holotype. Fig. 6. *Diapha candida* n.sp., specimen 6/1974, fore wing. Holotype. Fig. 7. *Diapha candida* n.sp., specimen 7/1974, hind wing. Fig. 8. *Permodiapha carpenteri* n.sp., specimen 11/1974, fore wing.

at a point, or anastomosed as in Diaphanopteridae. Since the presence or absence of the MA-Rs anastomosis is no longer useful as the family character, the status of the Elmoidae as a separate family is questionable. However, since *Diaphanoptera,* the type genus of the family, is from Upper Carboniferous strata, and since its body structure is entirely unknown, it seems advisable to consider the families distinct at least until more is known about *Diaphanoptera.*

The generic classification used here is based mainly upon the presence or absence of MA-Rs anastomosis, the general shape of the wings, and the character of the Rs area, since these features have been found relatively stable in the related order Palaeodictyoptera (Kukalová-Peck, 1971). All specimens available are figured. The lettering of the veins is shown in figures 9 and 10.

Genus **Elmodiapha,** new genus[2]

Type species: *Elmodiapha ovata* n.sp., Lower Permian of Moravia.

Fore wing: MA and Rs not anastomosed, connected by a cross vein. Wings elongated, oval in shape. Sc terminating on R shortly beyond mid-wing. Rs area large, with about 6 branches. R sending off a series of long branches beyond the end of Sc. Hind wing not known.

Elmodiapha differs from *Parelmoa* in having more elongate wings and richly branched Rs. From *Pseudelmoa* it differs in the shorter Sc, and in MA approaching more closely to Rs.

Elmodiapha ovata n.sp.

Figure 1, 2

This species is represented by two detached fore wings with a richly branched Rs.

Fore wing: length 17.5-21 mm, width 5.4-6.6 mm. Costa serrated. Rs with 6 long, densely arranged branches. MA simple, MP twice forked. CuA and CuP simple. 1A usually with a series of branches, anal veins sometimes branched.

Holotype: No. 1/1974 (fore wing fragment, length 18.5 mm, width 6.6 mm, obverse); specimen No. 2/1974 (fore wing fragment, length 16 mm, width 5.4 mm, obverse and reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

[2]The latter part of this generic name (and that of the other genera which are proposed in this paper) is derived from the Greek adjective *diaphanes* (distinct); it is treated as a noun and is considered feminine.

Genus **Protodiapha,** new genus

Type species: *Protodiapha maculifera* n.sp., Lower Permian of Moravia.

Fore wing: MA and Rs connected with a very short cross vein. Wings short and broad, broadest at about mid-wing. Posterior margin convexly bent, forming a lobe. Sc terminating on R shortly beyond mid-wing. Rs area small, with about 5 branches. Hind wing similar, but shorter, with the lobe on the posterior margin probably more pronounced.

Protodiapha differs from all the other genera which lack the anastomosis between MA and Rs by the presence of the lobe on the posterior margin.

Protodiapha maculifera n.sp.

Figure 3, 4

This species is established upon hind wings having a prominent lobe on the posterior margin and circular, cuticular spots on the wing membrane.

Hind wing: length 14 mm, width 4.5-5 mm. Wing broadest before the level of the end of Sc. The lobe on the posterior margin extending to the end of CuP. C with a series of long setae. Rs almost straight, with 5 branches. MA simple, MP with a fork. CuA simple, CuP sometimes with short branches. Anal veins with few branches. Thickened cuticular spots present.

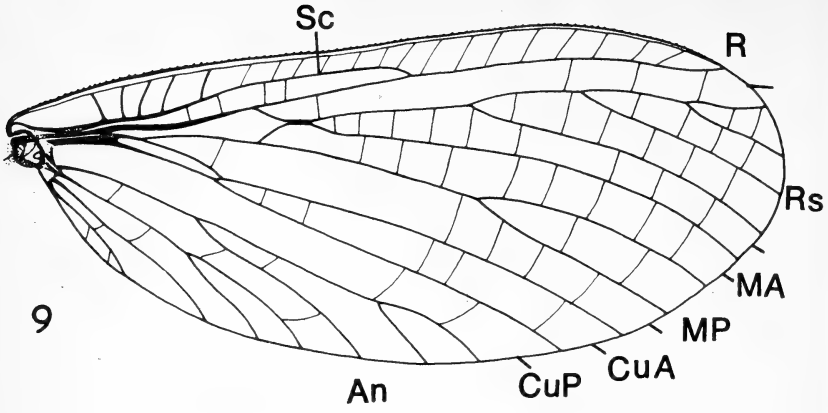
Holotype: No. 3/1974 (hind wing, length 13.5 mm, width 4.5 mm, obverse); specimen No. 4/1974 (hind wing fragment, length 8.3 mm, width 5 mm, obverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Protodiapha lineata n.sp.

Figure 5

This species is monotypic and based on the proximal half of a fore wing. However, the unique S-shaped cross veins accompanied by dark spots separate the species distinctly from all other Elmoidae.

Fore wing: length of the fragment 11.4 mm, width 5.8 mm. Wing broadest beyond the level of the end of Sc. The small lobe on the posterior margin extending to the end of CuP. Veins darkly colored. CuA with a short branch, CuP simple. Anal veins with few branches. Cross veins long, S-shaped, surrounded by dark spots. Circular cuticular spots absent.



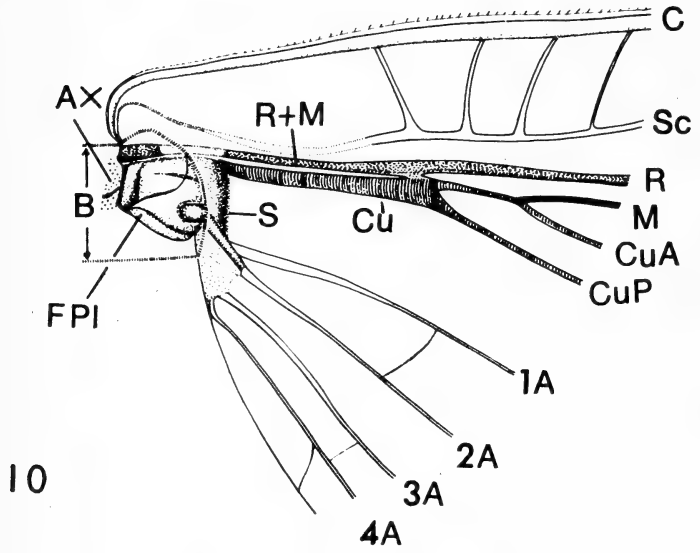


Fig. 9. *Permodiapha carpenteri* n.sp., specimen 8/1974, hind wing. Holotype. Fig. 10. *Permodiapha carpenteri* n.sp., specimen 8/1974, hind wing. Holotype. Ax = axillary sclerite; B = basal fold; FPl = fused basal plate; S = sclerotized region.

Protodiapha lineata differs from *maculifera* in having the wings widest beyond mid-wing, a smaller lobe on the posterior margin and long, S-shaped cross veins.

Holotype: No. 5/1974 (fore wing fragment, length 11.4 mm, width 5.8 mm, obverse). Paleontological Institute of Charles University, Prague, Czechoslovakia).

Genus **Diapha,** new genus

Type species: *Diapha candida* n.sp., Lower Permian of Moravia.

Fore wing: MA anastomosing with Rs for a short distance. Wings slightly broadened beyond mid-wing. Posterior margin concave. Sc terminating on R shortly beyond mid-wing. Rs with 5-6 branches. Hind wing shorter and probably narrower, with anal veins less branched. *Diapha* differs from the other genera described herein by the shape of the wings.

Diapha candida n.sp.

Figure 6, 7

A detached fore wing and a hind wing are referred to this species. The hind wing differs slightly in the outline of the posterior margin and in the thinner membrane. It may belong to a different species.

Fore wing: length 19 mm, width 5 mm. Wing broader in the distal half. C basally with a series of more prominent setae. Stem of R distinctly swollen next and distally from the basal fold. Rs concavely bent in the apical part, with 6 branches. MA simple, MP forked. CuA simple, CuP simple or with a branch. 1A with several branches, anal veins sometimes branched.

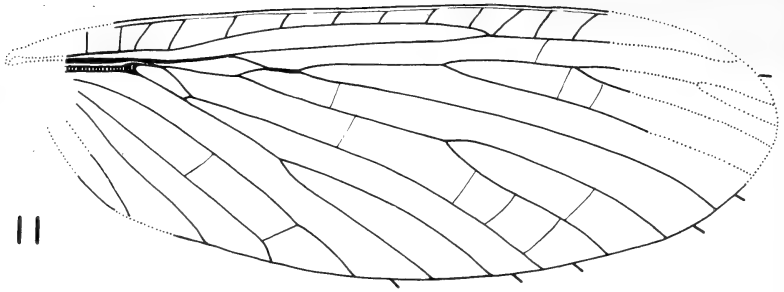
Hind wing: length 14 mm, with 4.2 mm. Wing membrane very thin.

Holotype: No. 6/1974 (fore wing, length 18.7 mm, width 5 mm, obverse); specimen No. 7/1974 (hind wing, length 14 mm, width 4.2 mm, obverse and reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Genus **Permodiapha,** new genus

Type species: *Permodiapha carpenteri* n.sp., Lower Permian of Moravia.

Fore wing: MA touching Rs or anastomosing with Rs for a short distance. Wing very broad. Posterior margin evenly concave. Sc terminating on R shortly beyond mid-wing. Rs with 3-4 branches. Hind wing similar to fore wing, but broader.



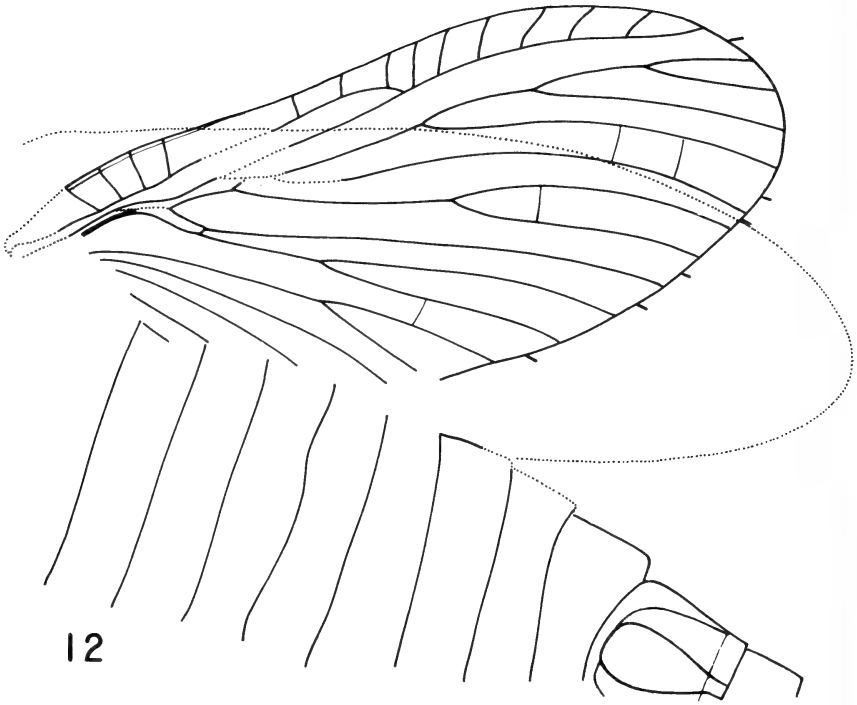


Fig. 11. *Permodiapha lata* n.sp., specimen 10/1974, fore wing. Fig. 12. *Permodiapha lata* n.sp., specimen 9/1974. Hind wing, fore wing outlined. Holotype.

Permodiapha differs from all other genera with MA-Rs anastomosed by its very broad wings.

Permodiapha carpenteri n.sp.[3]

Figure 8, 9, 10

A detached fore wing and a hind wing are referred to this species. The hind wing No. 8/1974 has been chosen as the holotype because of its well preserved base. The structure of the wing base are discussed above with the family characters.

Fore wing: length about 16 mm, width 5.3 mm. Wing large, with relatively strong membrane, veins and cross veins. Apex probably rounded as in the hind wing. Rs sending off 4 branches, slightly S-shaped distally. MA simple, MP with a long fork. CuA simple, CuP simple or forked. Anal veins with several branches. Fore wing about equally long but narrower than the hind wing.

Hind wing: length 16.3 mm, width 6.8 mm. Similar to the fore wing but broader, and narrowing more towards the base.

Holotype: No. 8/1974 (hind wing, length 16.3 mm, width 6.8 mm, obverse and reverse); specimen No. 11/1974 (fore wing fragment, length 11 mm, width 5.3 mm, reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Permodiapha lata n.sp.

Figure 11, 12

The species is represented by the holotype, probably a male, consisting of a vaguely preserved fore wing, well preserved hind wing and part of the abdomen, and by a detached wing, probably a fore wing.

Fore wing: length about 12.6-15.5 mm, width 4.9-5.2 mm. Wing membrane very delicate, cross veins almost invisible. Apical part of the wing somewhat narrower than in *carpenteri.* Rs curved posteriorly, sending off 4 branches. MA and CuA simple, MP and CuP with a long fork. Anal veins with few branches. Fore wing longer and narrower, with the apical part more pointed than the hind wing. Hind wing: length about 14.5 mm, width 6 mm. Anterior margin strongly curved towards the apex.

Permodiapha lata differs from *carpenteri* in having a very thin membrane and narrower fore wings.

[3]This species is named for Dr. Frank M. Carpenter (Harvard University), who has published extensively on the Diaphanopterodea.

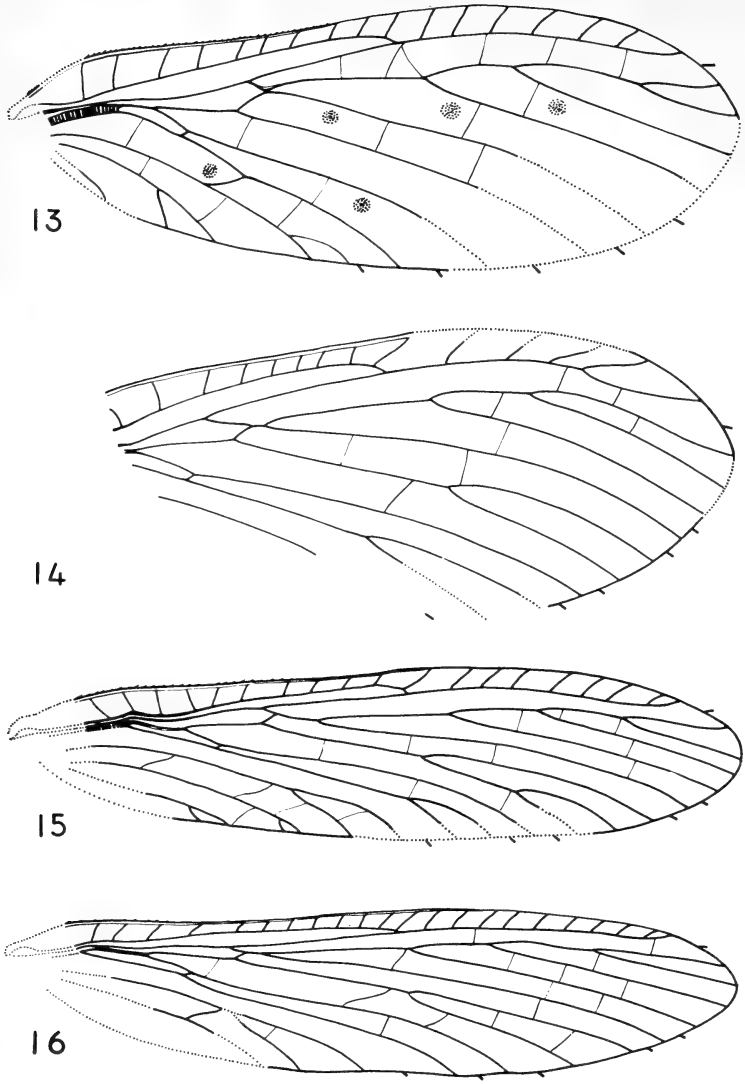


Fig. 13. *Permodiapha specula* n.sp., specimen 13/1974, fore wing. Holotype. Fig. 14. *Permodiapha* sp., specimen 14/1974, hind wing. Fig. 15. *Stenodiapha angusta* n.sp., specimen 17/1974, fore wing. Holotype. Fig. 16. *Stenodiapha angusta* n.sp., specimen 18/1974, fore wing.

Holotype: No. 9/1974 (fore wing, length about 15.5 mm, width 5.2 mm; hind wing fragment, length 13 mm, width 6 mm; abdomen, 1.-10. segment, length 13.5 mm; hind tibia, length 3 mm; obverse); specimen No. 10/1974 (fore wing fragment, length 12.6 mm, width 4.9 mm, obverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Permodiapha specula n.sp.

Figure 13

This species is monotypic and based upon a fore wing.

Fore wing: length 13.3 mm, width 4.8 mm. Wing relatively small, with very thin wing membrane. Cross veins almost invisible. Proximal half of the wing much narrower than the distal half. Venation very simple, seldomly branched. MA only touching Rs at a point. Rs sending off 4 branches, Rs S-shaped distally. MA, MP, CuA and CuP simple. Anal veins mostly simple. Circular cuticular spots present.

Permodiapha specula differs from *carpenteri* and *lata* in having the smallest wings with the most simple venation; in having the wings narrowed in the proximal half; and in the presence of the circular cuticular spots.

Holotype: No. 13/1974 (fore wing, length 13.3 mm, width 4.8 mm, obverse and reverse). Paleontological Institute of Charles University, Czechoslovakia.

Permodiapha sp. specimen No. 14/1974 (fig. 14) (hind wing fragment, length 11 mm, width 4.5 mm, obverse and reverse) might represent a separate species within the genus *Permodiapha,* but the fragment does not provide enough features for specific diagnosis.

Genus **Stenodiapha,** new genus

Type species: *Stenodiapha angusta* n.sp., Lower Permian of Moravia.

Fore wing: MA anastomosed with Rs for a short distance. Wing narrow, elongate, with main veins obliquely oriented. Sc terminating on R shortly beyond mid-wing. Rs with 3-4 branches, rs area long and narrow. Hind wing similar to the fore wing, but shorter and broader.

Stenodiapha differs from all other genera with MA-Rs anastomosed by the longest and narrowest wings, with the veins most obliquely oriented.

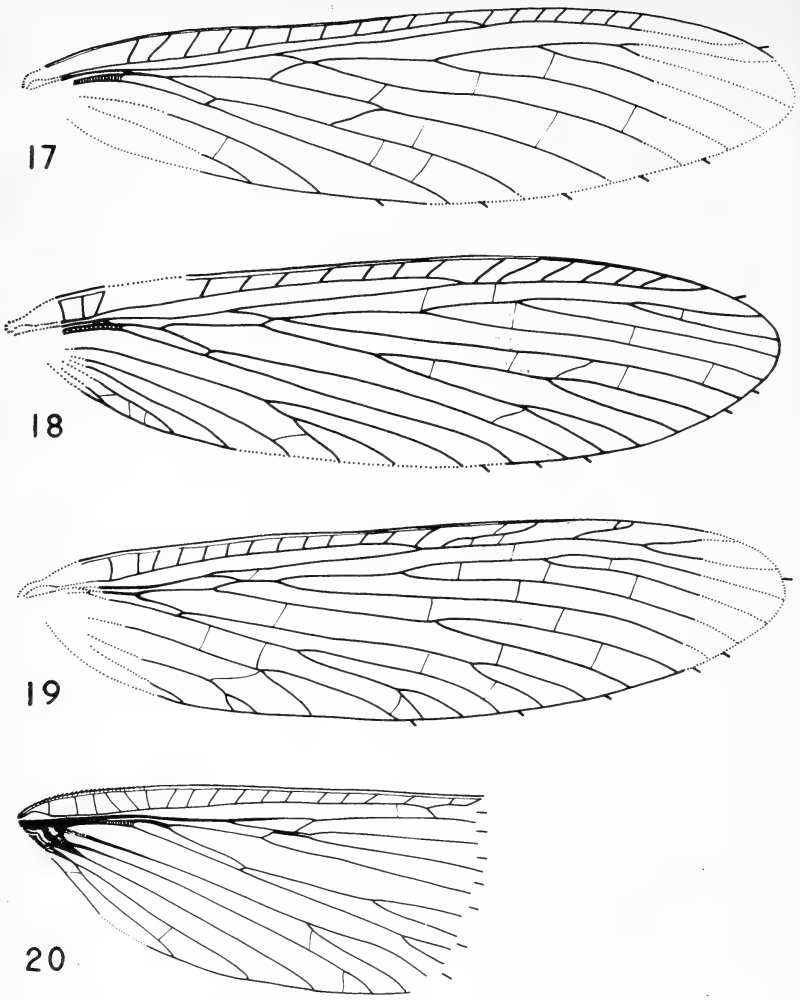


Fig. 17. *Stenodiapha angusta* n.sp., specimen 19/1974, fore wing. Fig. 18. *Stenodiapha angusta* n.sp., specimen 20/1974, hind wing. Fig. 19. *Stenodiapha moravica* n.sp., specimen 21/1974, fore wing. Holotype. Fig. 20. *Stenodiapha moravica* n.sp., specimen 22/1974, fore wing.

Stenodiapha angusta n.sp.

Figures 15, 16, 17, 18

Three detached fore wings and one hind wing are referred to this species.

Fore wing: length 17.2-20 mm, width 3.8-4.3 mm. Wing broadest at mid-wing, narrowing proximally. Wing membrane very thin. Rs with 4 long branches. MA simple, MP simple; CuA simple, CuP simple or forked. Anal veins with few branches or simple. Hind wing: length about 16.5 mm, width 4.4 mm. Similar to the fore wing, but shorter. In hind wing No. 20/1974, the richly branched MP is reminiscent of the Carboniferous genus *Diaphanoptera.*

Holotype: No. 17/1974 (fore wing fragment, length 18.2 mm, width 4.3 mm, obverse); specimen No. 18/1974 (fore wing fragment, length 15.7 mm, width 3.8 mm, obverse and reverse); specimen No. 19/1974 (fore wing fragment, length 14.6 mm, width 3.8 mm, obverse and reverse); specimen No. 20/1974 (hind wing fragment, length 15 mm, width 4.4 mm, obverse and reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Stenodiapha moravica n.sp.

Figure 19, 20

This species is based on two detached wings, probably fore wings.

Fore wing: length about 20.7 mm, width 5.3 mm. Wing broadened slightly at mid-wing. C serrated, basally carrying a series of setae. R sending off anteriorly several long twigs beyond the end of Sc. Rs with 3 long branches. MA simple, MP forked. CuA and CuP forked. Anal veins with few branches or simple.

Stenodiapha moravica differs from *angusta* in having the wings broader in the basal third and in the presence of long twigs on R beyond the end of Sc.

Holotype: No. 21/1974 (fore wing fragment, length 19.2 mm, width 5.3 mm, obverse and reverse); specimen No. 22/1974 (fore wing fragment, length 11.5 mm, width 5.3 mm, obverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Paradiapha, new genus

Type species: *Paradiapha delicatula* n.sp., Lower Permian of Moravia.

Fore wing: MA joining Rs for a short distance. Wing broadest at about the end of the second third, narrowing abruptly at the base. C serrated. Sc terminating on R shortly beyond mid-wing.

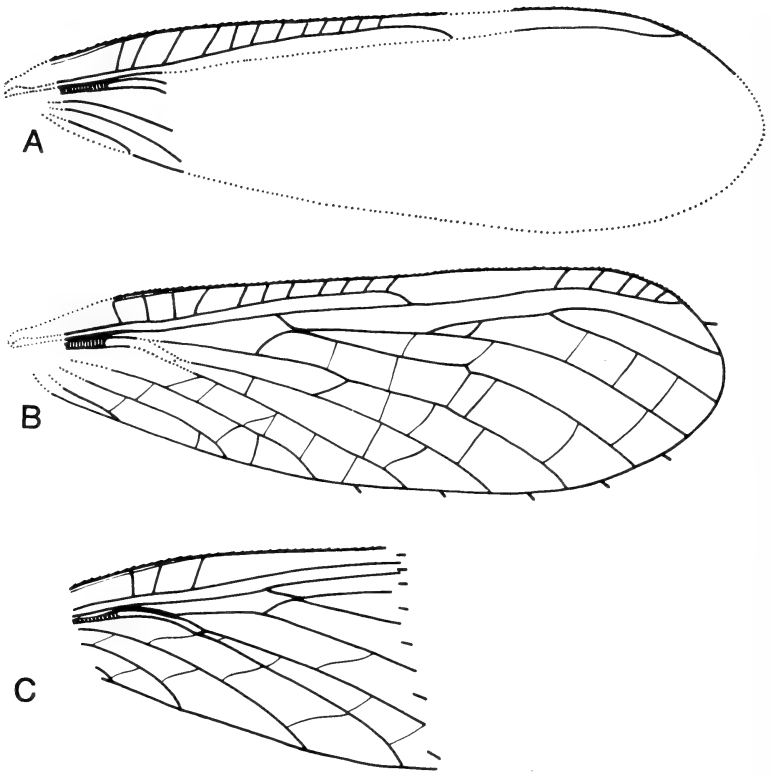


Fig. 21. *Paradiapha delicatula* n.sp., specimen 15/1974. Holotype. A. right fore wing, B. left hind wing, C. right hind wing.

Rs area small, with about 3 Rs branches. Hind wing similar to the fore wing, slightly shorter and broader proximally.

Paradiapha has a similar wing shape to *Parelmoa,* from which it differs in having a shorter Sc and by having MA almost anastomosed with Rs. From all other genera it differs in the wings being very broad in the distal third.

Paradiapha delicatula n.sp.

Figure 21, 22

The species is based upon two specimens. The holotype consists of the fragment of the right fore wing, of an almost complete left hind wing, and of the basal third of the right hind wing, all in partly folded position. Specimen No. 16/1974 is represented by the fragments of overlapping fore and hind wings, broad pterothorax and a remnant of the hind leg, with prominent setae on the tibia.

Fore wing: length about 12.9 mm, width about 4.3 mm. Wing membrane very thin. Anterior margin strongly bent apically, apex shifted posteriorly. C serrated, with a series of long setae. Rs strongly curved posteriorly, sending off 3 branches. MA, MP, CuA, CuP and anal veins simple. Hind wing almost identical with the fore wing, slightly shorter.

Holotype: No. 15/1974 (right fore wing fragment, length 12.6 mm; left hind wing fragment, length 12.8 mm, width 4.3 mm; right hind wing fragment, length 7.4 mm, width 4 mm; reverse); specimen No. 16/1974 (fore wing fragment, length 8.7 mm; hind wing fragment, length 6.2 mm; hind tibia, length 1.8 mm; obverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

Discussion

On superficial examination, the wing base in *Permodiapha* does not differ from the generalized neopterous type. The axillary region penetrates deeply into the wing, from which it is separated by the basal fold. However, careful study reveals that instead of the second and third axillary sclerites, which would be located proximally from the basal fold in true Neoptera, there is a large basal plate which is characteristic of the Paleoptera. The true axillary sclerite (fig. 9,Ax), perhaps homologous with 2Ax in Ephemeroptera (*sensu* Tsui and Peters, 1972), is located much more distally, in the "paleopterous" position.

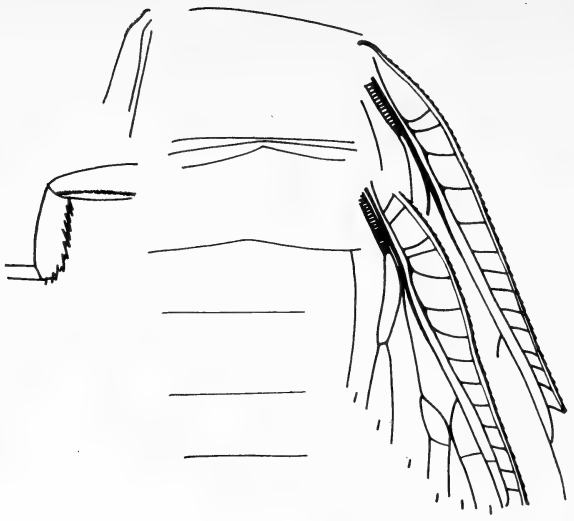


Fig. 22. *Paradiapha delicatula* n.sp., specimen 16/1974. Fore wing and hind wing, hind leg.

With the subcostoanal basal plate of advanced Palaeodictyoptera (Kukalová, 1970), the basal plate of Diaphanopterodea is only partially homologous. It is apparently formed only by the fused cubitoanal plate or eventually by the mediocubitoanal plate in which subcostal and radial basal plates do not participate. This condition is reminiscent of the "prefusion" stage of basal plates, known in primitive Palaeodictyoptera (Kukalová, 1960), from which Diaphanopterodea are supposedly derived.

The diaphanopteran wing base developed, in all probability, from the ancient paleopterous base, at the stage when the basal plates of the main veins were still separated, as indicated in some ancient Palaeodictyoptera. While the subcostal and radial plate became completely reduced to give place to the basal fold, the cubital and anal (or median, cubital, and anal) plates gradually fused and became separated from the wing by the basal fold.

The ability to penetrate narrow spaces for feeding and protection was undoubtedly a major factor in the success of Neoptera. The Diaphanopterodea, although having a wing-folding mechanism of their own, had highly specialized, haustellate mouthparts, as did their relatives, the Palaeodictyoptera and Megasecoptera. None of these paleopterous orders were apparently able to compete success-

fully with the more diversified Neoptera and none have been found so far in strata formed after the close of the Permian Period.

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OBSERVATIONS OF THE NESTING BEHAVIOR OF *RUBRICA SURINAMENSIS* (DEGEER) (HYMENOPTERA, SPHECIDAE)

By H. E. Evans,[1] R. W. Matthews,[2] and E. McC. Callan[3]

Introduction

Rubrica surinamensis (DeGeer) is one of the most familiar and well-studied digger wasps of South America. Yet the published accounts of its nesting behavior present a number of puzzling features. For example, Brèthes (1902) and Llano (1959) reported that females clean the cells of uneaten parts of flies and other debris, but others have not confirmed this. There are many records of females preying upon flies, but Callan (1950) has reported the occasional use of Lepidoptera and Odonata, a striking exception to the usual prey constancy of solitary wasps. Also Brèthes (1902) reported that the cocoons contain only two pores, although other Bembicini in this size range make 5-10 pores per cocoon. A fuller summary of published observations has been presented by Evans (1966).

In the hope of clarifying these and other problems relating to this widely distributed and apparently very successful species, the three of us have pooled our notes on three widely separated populations. One of us (EMC) resided in Trinidad for several years, and had an opportunity to observe a nesting aggregation in the hard, sandy driveway of his house near the Imperial College of Tropical Agriculture at St. Augustine, a residential area about 13 km east of Port of Spain. Two of us (HEE and RWM) visited Colombia and Argentina in January and February, 1972, and encountered the species in some abundance in both countries. Studies in Colombia were conducted on a large aggregation in a hard, gravel road on a denuded and eroded hillside just west of the city of Cali. In Argentina, we found three smaller aggregations in diverse situations within one day's drive of the city of Tucumán. Thus if any of the puzzling features of the behavior of this species bear a relationship to geog-

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raphy, to substrate, or to population density, the following synthesis of our notes from these various localities may serve to clarify this relationship. We also include a description of the larva and of the cocoon, in the hope of shedding light on the relationship of *Rubrica* to other genera of Bembicini.

Distribution and Ecology

R. surinamensis ranges from Trinidad and southern Mexico to central Argentina, being absent only from forested areas, higher mountains, and the friable sand of dunes and beaches. Because of its propensity for nesting in roads and paths, often in populated areas, it is one of the most commonly observed of solitary wasps, and its large size (17-24 mm) and pattern of yellow maculations against a rufous and fuscous background render it especially likely to attract attention. Since this species is subject to much variation in color, it should be pointed out that the populations we studied were all "typical of the species", that is, without discal yellow markings on the mesocutum or other unusual features. We found no consistent differences in color or structure between Argentinian wasps and those from northern South America, despite behavioral differences to be pointed out below.

As noted above, the aggregations at Cali, Colombia, and at St. Augustine, Trinidad, both occupied hard-packed roads. At Cali, an estimated 150 females nested along the road for a distance of about 25 m, many nests being separated by 0.5-1 m, but some clustered so that entrances were only 3-15 cm apart. The soil here is best described as clay-sand containing many small stones. At St. Augustine, the nesting aggregation varied seasonally from about a dozen to an estimated 50 individuals. These occupied an area of about 50 m^2, with nest entrances 25 cm to 1 m or more apart. The wasps occupied the same site at least from 1941 to 1944. The aggregation at Cali is also known to have persisted at the same site for several years.

On Trinidad, *R. surinamensis* has also been found nesting at the Erin Savanna, an area of open, virtually uninhabited country surrounded by evergreen seasonal forest, typical of the sandy soils of the south of the island. Here it nested in company with *Stictia pantherina* (Handlirsch). At other sites, *R. surinamensis* has been found nesting essentially alone, as few other bembicine wasps are adapted for digging in so hard a substrate.

The three small aggregations near Tucumán, Argentina, were in diverse situations. At Yacochuya, 8 km northwest of Cafayate, Salta,

some 20-30 females nested in a bare area measuring about 4 × 8 m, which had been cleared of rocks and vegetation, possibly for projected agriculture, in scrubby woodland in the foothills. The soil was a moderately friable, sandy loam. One additional nest was located in much harder and coarser soil in a schoolyard 0.5 km away. At Santa Maria, Catamarca, several nests were discovered in bare, firm, sandy loam in vacant lots in the city. At Las Termas de Rio Hondo, Santiago del Estero, six nests were found in coarse, hard-packed, sandy clay close to the banks of the Rio Dulce.

The three sites in Argentina were all in areas of low rainfall, and were notably dry during the period of study. Collecting records suggest that *Rubrica* is active here only during the warm summer months (chiefly December-April). In Trinidad, wasps were collected at almost all times of the year. Nesting activities, however, occurred mainly toward the end of the wet season and during the dry season, that is, December through May.

Male Behavior

In Argentina, males were frequently seen visiting various flowers, along with many females, but we observed no mating here. At Yacochuya, two males were seen consistently in the nesting area, and these males made several attempts to mate with females that were digging or opening or closing their nests. Much of the time these males flew about close above the ground and perched here and there with their wings partially extended. We saw no males at all in the large aggregation at Cali, Colombia.

At St. Augustine, Trinidad, males were occasionally seen flying in the immediate vicinity of the nesting site. More usually they were seen resting and apparently sunning themselves on nearby vegetation. Similar observations were made by Vesey-Fitzgerald (1940), who also reported that males and females rest on vegetation at night, the two sexes separately, the males "in groups of many individuals together." Bodkin (1917) also reported large sleeping clusters, of unspecified sex, in Guyana. At Cali, Colombia, we searched surrounding vegetation carefully in the evening, but were unable to find such clusters. It was clear, however, that females do not spend the night in the nests and males do not dig "sleeping burrows," as is the case in *Bembix*.

Nest Construction

Females dig effectively through the firm and often coarse substrate,

using the mandibles to cut through the soil and to haul out small stones, the front legs to scrape loosened soil beneath the body (Fig. 1). Apparently the better part of one day is required for completion of a nest. When the burrow and cell are complete, the female partially disperses the mound of soil and constructs a rounded pile of soil over the entrance. This pile serves as a perch to which she returns intermittently as long as the nest is active (Fig. 3). Since this "pile-building" behavior is, so far as we know, unique, we present in some detail our notes on a typical individual at Cali (RWM, note C6).

This female was observed digging steadily from 1030 to 1100 hours on 11 January 1972. She then came out, made a closure, and flew off, leaving the accumulated soil intact. She returned more than an hour later, opened the nest, and resumed digging. She spent much time in the burrow, from time to time emerging and scraping soil onto the mound, then re-entering to dig further. At 1358 she came out, closed the entrance, and walked slowly to the end of the mound, where she turned in a circle several times while scraping sand in all directions. After spending 3 minutes leveling in this manner she flew off, returning 5 minutes later with a small fly. In 25 seconds she emerged from the nest, turned around outside and immediately re-entered, remained inside 35 seconds, then came out again. This sequence of going in and coming out was repeated 11 times. (Several other females were seen to exhibit similar behavior, which we assume to play a role in familiarizing the wasp with the new nest.)

Following this the female made a strong outer closure, packing the soil with vigorous blows of the tip of the abdomen, and then resumed leveling. She did this by walking to the end of the mound while scraping soil back toward the entrance, then turning around and walking to the entrance without scraping; then turning around again and walking to the end of the mound scraping soil. This was repeated many times over a 12-minute period, the result being removal of most of the soil to a heap over the entrance. The wasp dragged several pebbles onto this pile and periodically tamped it with the tip of her abdomen. Eventually she made several short flights; each time she returned adding a little more soil to the pile, which now measured 35 mm × 25 mm × 7 mm deep in the center.

We observed similar behavior on many occasions at Cali. Often the pile was surrounded by a ring of smooth soil, where the loose surface soil had been scraped upon it. The original mound, resulting from the digging of the nest, was sometimes partially in evidence,

Figs. 1-3. *Rubrica surinamensis* females nesting in a hard-packed gravel road near Cali, Colombia. (1) Digging the nest. (2) Entering the nest through the entrance pile, carrying a paralyzed fly beneath the abdomen. (3) Resting on the entrance pile during an inactive period.

often forming a rather flat, fan-shaped area as much as 16 cm wide and extending as much as 14 cm from the entrance. The pounding movements, made with the tip of the abdomen when making the pile and at each nest closure, were sometimes audible up to 3 m away. The entrance piles were used as periodic perches to which the females returned off and on throughout the day. We rarely observed aggression between females on adjacent piles, and we do not regard them as territorial perches.

Many details of this behavior were confirmed in Argentina, but some differences were noted. At Yacochuya, leveling of the mound seemed not to occur, the wasps merely scraping soil from the immediate vicinity of the hole when making the pile over the entrance. Thus each nest came to be marked by a small pile surrounded by a smooth area 2-4 cm across, and finally, on one side, the remains of the mound, usually 7-8 cm wide × 10-13 cm long × 1-2 cm deep. We noticed several nests here that had short grooves or "back burrows" into the mound, only 1-2 cm deep. These were made at the time of temporary or final closures, and appeared to represent quarries for obtaining soil for fill. One nest at Las Termas, still active and containing a half-grown larva, had a well-defined accessory burrow 4 cm long, about 1.5 cm from the true burrow and at a right angle to it.

Nest Structure

The nest is a simple, oblique burrow with a terminal cell. All who have worked on this species have found the burrow to be very short (summary in Evans, 1966). Our studies confirmed this. One nest at St. Augustine had a burrow about 15 cm long ending in a cell about 3.5 cm long. Burrows at Cali averaged even shorter than this, although burrows at all three localities in Argentina were somewhat longer (Table 1). We attribute this to the fact that the soil at the Cali site was unusually hard. We found that cells when first made measured about 15 mm in diameter by 25-30 mm in length, but as the larva grew tended to be lengthened to as much as 4 cm.

In contrast to previously published observations, we found that nests were often multicellular. That is, after completing the provisioning of the initial cell, the female often made another cell from a short side-burrow of the same nest. Of the 22 nests excavated at Cali, 8 had one cell, 8 had two, 5 had three, and 1 appeared to have five (but we are not certain that all five belonged with this nest). The cells of any one nest were at about the same depth and were

Table 1. Nest structure of *Rubrica surinamensis*

Locality	No. nests	% multi-cellular	Burrow length (cm)*	Cell depth (cm)*
Cali, Colombia	22	64	11.8 (9-16)	7.3 (5-9)
Cafayate, Argentina	12	17	16.8 (15-18)	9.5 (8-11)
Santa Maria. Argentina	3	0	16.0 (15-18)	9.2 (8.5-10)
Las Termas, Argentina	6	0	16.3 (14-22)	10.5 (8-13)

* Mean and range of variation.

separated by only 1-4 cm of soil. It is, of course, possible that the unicellular nests we dug out might have had more cells added (except for one that had received the final closure). Four of the 2-celled nests and two 3-celled nests had received the final closure when excavated. In multicellular nests, the earlier cells invariably contained cocoons, but it was usually possible to trace the filled burrows to these cells because the fill was not as compact as the surrounding soil.

However, only 2 of 21 nests in Argentina were bicellular and none had more than two cells; one of the 2 bicellular nests was in the hard soil of the schoolyard at Yacochuya. There is a general tendency for wasps nesting in firm soil to make shallower nests and to prepare more than one cell per nest. Thus it would be rash to assume that these differences between the Colombian and Argentinian populations had a genetic basis.

There is no evidence that an inner closure, separating cell from burrow, is maintained at any time. However, an outer closure is normally made whenever the female leaves the nest. We noted no exceptions to this in Colombia or Argentina, but occasional individuals in Trinidad did omit the outer closure. This was also noted in Trinidad by Vesey-Fitzgerald (1940), who believed that closure was usually omitted when the larva was large.

Provisioning the Nest

There are many published records of *Rubrica surinamensis* preying upon flies, and our own records confirm the fact many kinds of flies of small to moderate size are accepted (Table 2). The flies are evidently killed by the sting. The egg is laid erect on the side of the first fly placed in the cell, and provisioning is progressive.

The flies taken are apparently those readily available near the nesting site. Belt (1874) observed females pursuing horseflies around

livestock and humans, and Callan (1945) reported the capture of engorged stable-flies, one nest having been provisioned entirely with stable-flies. The frequent use of stable-flies and Tabanidae in Trinidad probably reflects the fact that the cattle pens of the Imperial College of Tropical Agriculture were not far away. All specimens of Tabanidae and Muscidae from this site were females. On the other hand, the records of Syrphidae included males as well as females, suggesting that they were taken on flowers. There were many cattle near the nesting site at Cali, again possibly serving as a source of Muscidae, although no tabanids were found to be used as prey at this site or at any of the localities in Argentina.

We observed several females hunting beeflies at Santa Maria, Catamarca, Argentina (RWM, note no. C38). These wasps flew about flowers growing in the sand, apparently hunting flies visually. Having located a beefly, the wasp would hover some 30-40 cm behind it, about 15 cm above the sand, and follow the fly until it landed on a flower. Then it would dash suddenly at the fly, sometimes producing an audible clash. However, although more than 20 attempts to take beeflies were observed, in every case the fly darted almost straight up at the last moment and escaped from the wasp. The infrequent use of beeflies as prey (Table 2) may reflect their lack of success with flies of this group. At Santa Maria, *Rubrica* females were also seen to dash after *Microbembex* wasps visiting the flowers, again unsuccessfully.

The way in which the prey is carried to the nest is similar to that of other bembicine wasps. It is held firmly by the middle legs, ventral side up and with the head forward. Since the wasp must dig through the small pile of soil over the entrance, as much as 20-60 seconds may be required to gain entry (Fig. 2). As the wasp enters, the prey slides backward and the grasp is shifted to the hind legs, whereupon wasp and prey disappear down the burrow. However, flies are occasionally dropped or become stuck in the entrance. In such cases the wasp enters the nest, turns around inside, and comes out and drags the prey in with her mandibles. On leaving, the wasp makes a quick closure, then flies about briefly and returns one or more times to scrape soil over the entrance.

Both at St. Augustine, Trinidad, and Cali, Colombia, we noted instances in which females carrying prey were pounced upon by other females. This usually resulted in the females struggling on the ground and ended by one escaping and diving precipitously into her nest with the prey.

Table 2. Dipterous records for *Rubrica surinamensis*

Species of fly	Number of specimens		
	Trinidad	Colombia	Argentina
STRATIOMYIDAE			
Hedriodiscus chloraspis Wiedemann		1	2
H. pulcher Wiedemann		1	64
Hermetia illucens L.	6	2	
Hoplitimyia fasciata F.		4	8
H. subalba Walker	5		
Labostigmina inermis Wiedemann			15
Stratiomys connexa van der Wulp			4
TABANIDAE*			
Esenbeckia prasiniventris Macquart	1		
Leucotabanus exaestuans L.	1		
Tabanus nebulosus DeGeer	2		
T. claripennis Bigot	4		
T. lineola var. *carneus* Bellardi	2		
T. colombensis Macquart	4		
BOMBYLIIDAE			
Villa sp.			4
SYRPHIDAE			
Eristalis erraticus Curran	3		
E. sp. nr. *fasciatus* Wiedemann	4		
E. tenax L.			1
E. testaceicornis Macquart		1	
E. vinetorum F.		1	
E. sp.	8		
Quichuana aurata Walker	3		
Volucella obesa F.	9	7	
MUSCIDAE			
Morellia scapulata Bigot	1		
Musca domestica L.	8	1	
Stomoxys calcitrans L.	5	3	
SARCOPHAGIDAE			
Oxysarcodexia sp.		1	
Sarcophaga spp.	1		1
CALLIPHORIDAE			
Cochliomyia macellaria F.			4
Phaenicia sp.		2	
TACHINIDAE			
Cylindromyia sp.			1
Protogoniops sp.		2	
Ptilodexia sp.		9	

* Several of these records of Tabanidae were published by Bequaert (1944). His names are here updated according to Fairchild and Aitken (1960).

Use of Unusual Prey

Despite the many records of *R. surinamensis* taking flies (there are numerous published records as well as over 200 new records summarized in Table 2), we are now able to report 4 records of the use of non-dipterous prey, 2 from Trinidad and 2 from Argentina. We assume that these were in the nature of "mistakes," that is, that the wasp struck them in the course of fly-hunting and for some reason failed to discriminate them from their more usual prey. Since some of the Lepidoptera were found in cells only as wings, it is obvious that the bodies had been accepted as food by the larvae.

On 2 December 1941, at St. Augustine, Trinidad, EMC observed a female flying toward her nest carrying a dragonfly, *Perithemis moona* Kirby (Odonata, Libellulidae). This is a yellow-winged species with a body length of about 25 mm. As the prey was held well back, probably by the middle legs, it extended some distance behind the abdomen of the wasp. The wasp was caught with her prey, which was dead; the nest was unfortunately not located. On 11 March 1947, at St. Augustine, E. A. Fitzpatrick took a female that was carrying a small skipper butterfly, *Panoquina* sp. (Lepidoptera, Hesperiidae). The prey was dead when caught.

We found the wings of Lepidoptera in two nests at Las Termas, Santiago del Estero, Argentina (HEE, note nos. C63, 64). One nest contained the wings of a skipper (*Monca* sp., Hesperiidae) along with 3 flies and a half-grown larva. The other nest, only 2 m away, contained the wings of two moths (both probably *Loxostege* sp., Pyralididae). This cell contained many flies and a nearly full-grown larva.

Cell Cleaning

As noted in the introduction, two observers in Argentina have seen females flying from their nests carrying the remains of flies or bits of debris. However, this has not been reported by other workers. Although our studies of the aggregations in Trinidad and Colombia were fairly detailed, we did not observe this behavior, and the numerous nests excavated at Cali usually contained many fly remains with the larva or cocoon.

However, our experience at Yacochuya, near Cafayate, Argentina, was quite different. When we discovered this small aggregation on the morning of 2 February 1972, a number of females were seen to fly from their nests and drop small objects some distance away.

Studies over the next few days revealed that most females cleaned the cells of uneaten prey or pieces of prey each morning before they began provisioning. Wasps backed out of their burrows, holding the debris in their mandibles, then flew off 2-6 m, ascending to a height of 1-2 m, and dropped it on the ground. Many females flew over a nearby hedge and dropped their load on the other side. It appeared that smaller pieces of prey were dropped closer to the nest than larger ones (sometimes whole, uneaten flies), although we have no quantitative data to support this. Cell cleaning usually required only 5-8 minutes, during which time 3-6 loads were carried from the nest. The following notes on one nest (HEE, C55-2) may serve as an example.

This female first entered her nest at 1106 hours, clearing the entrance as she entered. After a minute or two she backed out with a large, whole fly which she carried on the wing a distance of 4 m and dropped. She returned to the nest quickly, this time remaining inside only 10 seconds and emerging with a fly which she carried 6 m and dropped from a height of 1.5 m. On the next trip she remained in the nest 10 seconds and emerged with a small particle which she dropped 3 m away from a height of 1.5 m. On the fourth and final trip she remained in the nest 8 seconds and emerged with a very small particle which she dropped quite close to the nest. She then returned to the nest, closed the entrance (having left it open while cleaning), and flew off at 1114. She returned with her first fresh prey at 1117.

We did not observe cell cleaning at Santa Maria or Las Termas, Argentina, but our observations were not prolonged in either site, and were mostly made in the afternoon. Most of the nests we excavated at these sites contained little debris, strongly suggesting that cell cleaning had occurred earlier in the day. We are under the impression that cell cleaning is a common feature in populations in western Argentina, as it evidently is in the Buenos Aires region (Brèthes, 1902; Llano, 1959).

Final Closure

Several final nest closures were observed at Cali, Colombia. In each case the female emerged from the entrance repeatedly while scraping soil behind her; she often moved as much as 4 cm away, scraping soil into the hole, then either backed in or turned around and walked to the burrow, turning around in the entrance and backing in. In no case were females seen to take flight and land in the

entrance, then turn around and back in, as occurs commonly in other sand wasps. Much use is made of the mandibles in biting soil around the entrance, the wasp often producing a loud buzz in the process. When the burrow is nearly full, it can be seen that the soil is packed in with rapid blows of the tip of the abdomen, which is turned downward and forward and moved in a somewhat circular pattern. Finally, small pebbles may be dragged backward over the entrance.

Nest Associates

The fly *Raviniopsis spinosa* (Hall) (formerly in the genus *Pachygraphomyia*) (Sarcophagidae), is a constant nest associate of *Rubrica surinamensis* in Trinidad, where it was first recorded by Vesey-Fitzgerald (1940). It has been noticed by EMC many times in Trinidad, and also on the Paria Peninsula of Venezuela (Callan, 1954). The fly was also common at Cali, Colombia, usually to be seen perched near a nest entrance on the alert for a wasp returning with prey. One was seen to dash quickly upon a fly just being brought into a nest, presumably larvipositing upon it. Six of 37 cells dug out at Cali contained maggots, 2-4 per cell. In every case the wasp larva appeared healthy, and several had attained full size.

None of the maggots found in cells at Cali were reared through to adulthood, but at St. Augustine, Trinidad, on 14 March 1943, EMC found a nest containing a maggot along with a large wasp larva. The maggot was fed on dead houseflies and pupated on 16 March, producing an adult *R. spinosa* on 28 March. On another occasion, at St. Augustine, a female *R. spinosa* was captured and 21 minute first instar larvae were squeezed from her abdomen. Some of these larvae were placed on a large *Rubrica* larva, but they made no attempt to attack it. Five of the maggots were placed separately in small glass vials. Two or three dead houseflies were put in each vial and others were subsequently added. Two of these larvae eventually pupated, producing adult *R. spinosa* 12-14 days later.

Other species of Sarcophagidae evidently also act as inquilines in *Rubrica* nests. One of several flies taken from nest entrances at Cali was identified as *Sarcophaga* sp. Three flies reared from nests at St. Augustine on 2 December 1941 proved to be *Sarcodexia sternodontis* Townsend. It should be noted that *Sarcodexia, Sarcophaga,* and *Raviniopsis* are all members of the subfamily Sarcophaginae, although it is Miltogramminae that are usually found associated with the nests of Hymenoptera.

Curiously, we found none of these Sarcophaginae in any of the study areas in Argentina. One fly noted trailing a *Rubrica* that was digging in a road near Yacochuya proved to belong to the genus *Senotainia,* of the Miltogramminae. One of 14 cells excavated at this locality contained 2 small maggots in debris surrounding a cocoon, but we did not rear these successfully. Brèthes and Llano made no note of inquilinous flies in eastern Argentina, and Brèthes noted that the cells he excavated contained little in the way of debris, doubtless the result of cell cleaning.

A minute fly of the family Chloropidae, *Liohippelates pusio* (Loew), was also recorded by Vesey-Fitzgerald (1940) in association with *R. surinamensis* in Trinidad. This fly has also been observed at St. Augustine in the immediate neighborhood of nests and also entering open burrows in the absence of the wasp. This fly is no doubt also a nest scavenger, and its larvae probably feed on the uneaten remains of prey left by the wasp larva.

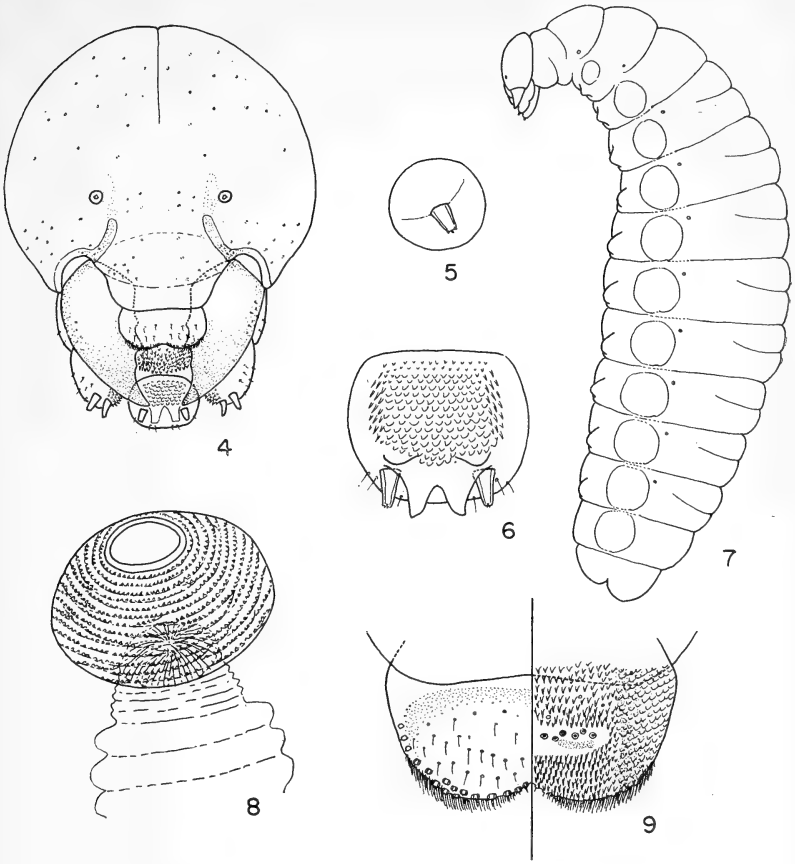
Structure of Cocoon

Ten cocoons of *R. surinamensis* were collected at Cali, Colombia, 2 more near Cafayate, Argentina. The cocoons from the two localities are very similar, and the following notes pertain to all 12. The cocoons are ovoid, more pointed at the posterior end, and have a hard wall made up of soil particles and salivary secretions, as usual in Bembicini. They vary in length from 25 to 28 mm (mean 26.7 mm) and in maximum width from 8.5 to 10 mm (mean 9.6 mm). The pores are more or less evenly distributed around the widest part and number from 4 to 6 (actually 5 of the cocoons we collected have 4, 4 have 5, and 3 have 6). Each pore is complex, being darkened and strongly elevated, some of them rising as much as 0.4 mm above the cocoon surface; each is somewhat bilobed, each lobe having several small protuberances, each of which terminates in a minute opening.

Brèthes (1902) reported only 2 pores per cocoon, an unusually low number for so large a cocoon, causing the species to occupy an anomalous position in the diagrammatic representation of cocoon size versus number of pores presented by Evans (1966, Fig. 209). Even 4-6 is a low figure for a cocoon of this size, but the fact that each pore has numerous small apertures may compensate for this.

Structure of the Mature Larva

There is no detailed published description of the larva of this



Figs. 4-9. Structures of full-grown larva of *Rubrica surinamensis*. (4) Head, anterior view. (5) Antennal orbit and papilla. (6) Labium, oral surface. (7) Body, lateral view. (8) Spiracle of most anterior pair. (9) Labrum (left) and epipharynx (right).

species, and since *Rubrica* is a somewhat unusual genus with respect to adult structure and behavior, it seems worth presenting a description of larval characters. Our description is based on 15 full-grown larvae from Colombia and Argentina. We noted no variation worthy of note and no differences between larvae from the two widely separate areas.

Length 30 mm; maximum width 8 mm. Body robust, more tapered anteriorly than posteriorly; terminal segment blunt, supra-anal lobe surpassing subanal; pleural lobes well developed; middle body segments weakly divided into two annulets dorsally; each segment except last two with a transverse ventral swelling (Fig. 7). Spiracular atria about .20 mm in diameter except second pair only .16 mm in diameter; external opening of atrium small, about .08 mm in diameter (second pair .07 mm), peritreme very narrow; walls of atrium lined with many rings of minute spinules; opening into subatrium large, armed with a strong circlet of spines (Fig. 8). Integument smooth, visibly setose only under high power; each segment dorsally with a few minute setae, longest measuring only .06 mm; parts of venter with sparse, weak spinules.

Head 1.9 mm wide, height (exclusive of labrum) 1.9 mm (Fig. 4). Parietal bands absent; antennal orbits very small, only .10 mm in diameter, papillae short, about .04 mm long, only slightly longer than basal width (Fig. 5). Front deeply impressed just mesad of each antennal orbit. Head with scattered minute punctures, some of them giving rise to minute setae, especially on clypeus. Labrum .70 mm wide, emarginate medially, disc with more than 40 rather strong setae as well as a number of non-setigerous punctures, apical margin strongly bristly, paralleled by a row of about 40 barrel-shaped sensilla; epipharynx strongly spinulose, but with a bare central band which bears six sensory pores on each side of the midline, also with several additional pores above the central band (Fig. 9). Mandibles .95 mm long, .5 mm wide at the base, tridentate and with a weak fourth tooth between the apical two; sides with several minute setae. Hypopharynx and mesal margins of maxillae densely spinulose; maxillae with several lateral setae; maxillary palpi and galeae subequal in length, the latter more slender, somewhat horn-shaped. Oral surface of prementum mostly papillose, with a few spinules laterally and basally; spinnerets barely exceeding labial palpi (Fig. 6).

The larva of *Rubrica* differs from that of nearly all other Bembicini in lacking all evidence of parietal bands and in having the spinules on the prementum confined to the sides and base. The short

antennal papilla and almost total lack of body setae and spinules suggest *Steniolia.* On the whole, larval characters suggest that *Rubrica* may not be as closely related to *Bembix* and to *Stictia* as might be assumed on the basis of adult structure.

Discussion

The somewhat isolated position of *Rubrica* among the genera of Bembicini is suggested not only by larval characters but by a number of behavioral peculiarities, of which the following five are especially noteworthy.

(1) Females make a small pile of earth and pebbles over the nest entrance, to which they return and use as a perch from time to time when not engaged in other activities. Members of other genera that spend inactive periods away from the nest tend to return occasionally, but usually hover briefly over the entrance (e.g. *Steniolia*).

(2) Although *R. surinamensis* is a predator on flies, there are several records of females taking Lepidoptera (Hesperiidae, Pyralididae) and one record of a dragonfly being used as prey (Libellulidae). Evidently the females do not discriminate as sharply as do most other Bembicini. For example, the many hundreds of records for North American *Bembix* include no non-dipterous prey (Evans, 1957, 1966). On the other hand, Janvier (1928) found that the fly predator *Zyzzyx chilensis* (Eschscholz) occasionally takes a skipper (Hesperiidae). Manfredo A. Fritz has informed us (in litt.) that he has taken skippers from the nests of the fly predator *Trichostictia guttata* (Taschenberg) in Argentina. It should be noted that Lepidoptera form the normal prey of members of the genera *Editha* and *Stictiella.* Use of Odonata as prey is more unusual, but two Australian species are now known to prey on damselflies, at least one of them also on flies (Evans and Matthews, 1973). Evidently there is enough similarity in the flight characteristics of Lepidoptera and Odonata to those of Diptera that the switch-over is not difficult.

Lin (1971) recently discovered that some members of an aggregation of 2000 females of *Stictia carolina* Fabricius in Oklahoma preyed not only upon skippers but upon small brown cicadas (Homoptera), although flies constitute the usual prey of this species. He postulated that competition for food in this dense population caused females to accept unusual prey.

(3) Cell cleaning by flying from the nest and dropping the debris some distance away is well marked in Argentinian populations, but it has not been observed in northern South America. It is perhaps

no coincidence that dipterous nest scavengers appear much more prevalent in Trinidad, Venezuela, and Colombia than they are in Argentina. We assume that cell cleaning has evolved in response to these nest associates, which probably often cause the female to bring in additional flies and thus prolong the nesting cycle. Cell cleaning is known in several species of *Bembix* (Evans, 1966, pp. 358, 451), although none of these wasps are known to carry the debris as far as *Rubrica* carries it.

(4) The mature larva constructs 4-6 pores in the walls of the cocoon, but these pores are complex, each consisting of a bilobed elevation containing several minute perforations. The construction of these pores has not been observed in *Rubrica,* and the function of the pores has not been clearly demonstrated in any bembicine wasps.

(5) Females spend the night away from the nest, and they have been reported to cluster on vegetation, although we have not observed this. Clustering is known in several genera of Bembicini, especially *Steniolia* and *Zyzzyx*. Species of *Stictia* and *Bicyrtes* also spend the night on vegetation, although in all known species of *Bembix* the female sleeps in the nest, and in *Microbembex* the female sleeps in a short burrow apart from the brood nest.

Thus on the whole behavioral and larval features present a somewhat ambiguous picture as to the relationships of *Rubrica* to other genera, although they do emphasize that it is a distinctive taxon not closely related to *Bembix*. Of particular interest is the intraspecific variation in the behavior of *R. surinamensis*. The occasional use of non-dipterous prey suggests a loosening of the stereotypy of hunting behavior, in the direction of the broad-spectrum prey selection of some species of *Glenostictia* or of the total lack of specificity of all species of *Microbembex*. Cell cleaning in *R. surinamensis* appears to be an example of geographic variation in behavior, populations in the southern parts of the range apparently having evolved a mechanism for reducing the success of nest scavengers that northern populations have not evolved (at least so far as presently known). Nest depth and number of cells are probably related to hardness of the substrate, shallow nests with several cells being an adaptive response to very hard soil, reducing the time and wear involved in nest construction. All of these points are deserving of further study by persons with aggregations of the species at their disposal. *Rubrica surinamensis* is evidently one of the most successful of South American solitary wasps, and a more thorough knowledge of its biology may teach us much about the origin and adaptiveness of behavioral attributes.

Acknowledgments

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A NEW SPECIES OF *OPITHES* FROM MEXICO WITH A KEY TO THE SPECIES (COLEOPTERA: STAPHYLINIDAE)*

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The generic name *Ophites* was validated by Erichson (1839, p. 29) by inclusion in a key to the genera of the tribe Paederini. In the second half of the same work (1840, p. 627) Erichson described in detail the genus and three included species from Colombia. Sharp (1876) added a new species from Brazil and Lynch-Arribálzaga (1884) added another from Argentina. In 1901 Fauvel described a sixth species from Colombia. In 1952 Blackwelder called attention to the fact the name *Ophites* was preoccupied by Wagler, 1830, and proposed the substitute name *Opithes*.

In 1904 Fauvel described from Brazil two genera, *Mimophites* and *Bolbophites,* which closely resemble *Opithes*. Members of each of these genera have the slender neck and narrow pronotum of *Opithes*. Blackwelder in 1944 placed the former next to Ophites (= *Opithes*) and the latter far removed in the subtribe Echiasteres. Seevers (1965) reviewed *Mimophites* and *Bolbophites*. He stated "*Mimophites* appears to belong to Casey's (1905) subtribe Stilici, a group included in Blackwelder's (1944) Lathrobii." In *Opithes* the first antennal segment is as long as the next six combined, more than one-third of the length of the entire antenna; the gular sutures are narrowly but distinctly separate; the neck is about one-fourth the length of the head and the last segment the maxillary palpus is not subulate but is almost as wide at base as the apex of the third segment and is conical. *Mimophites* differs from *Opithes* in that the first antennal segment is short, no longer than the next two combined, and the antennae are not anteriorly flexile; the neck is short; the gular sutures are united and the last segment of the maxillary palpus is subulate and quite slender. *Bolbophites* differs from *Opithes* in that the first antennal segment is no longer than the next three together; the gular sutures are united and the last segment of the maxillary palpus is subulate.

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Bolbophites is placed in the subtribe Echiasteres because the prosternum is produced posteriorly and thence expanded laterally to the hypomera, a character which is usually concealed by the anterior coxae and consequently difficult to see. It is readily distinguished by the pronotum and elytra being provided with large, conspicuous knobby protrusions. *Mimophites* includes several species. Borgmeier (1949) reviewed the genus and provided a key to the species. Fauvel (1904) included two species in *Bolbophites* at the time he described the genus. No species have been added since.

Blackwelder (1939) included *Ophites* (= *Opithes*) in a key to the genera of the subfamily Paederinae where he indicated its close relationship to *Homaeotarsus* by the presence of geniculate, anteriorly flexile antennae. Specimens of *Mimophites* and *Bolbophites* apparently were not available to Blackwelder as he did not include them in his key.

In this work I describe a new species of *Opithes* from Mexico and for the first time present a key to the species of the genus.

Nothing has been recorded concerning the habits of the various species nor of the habitats in which they are found. Unfortunately, Mr. Crandall cannot recall the circumstances under which he captured the specimen described here from Mexico.

Key to the species of *Opithes* Blackwelder

1. Head and pronotum ferrugineus. 2
   Head and pronotum black or piceus. 3
2. Surface of head anterior to eyes with two foveae, length 12mm.; Mexico. ..... *crandalli* new species
   Surface of head anterior to eyes with three foveae, length 10 mm.; Argentina. ..... *fauveli* Lynch-Arribálzaga
3. Head and pronotum opaque. 4
   Head and pronotum shining. 5
4. Abdomen densely opaque; Brazil. ..... *stilicoides* Sharp
   Abdomen semi-shining; Columbia. ..... *velitarsis* Erichson
5. Tibiae in part pale. 6
   Tibiae entirely black; Columbia. ..... *versatilis* Erichson
6. Elytra black; Columbia. ..... *raphidioides* Erichson
   Elytra aeneus; Columbia. ..... *bugnioni* Fauvel

Opithes crandalli new species

Description of holotype.

Color. — Head, pronotum and first four and one-half abdominal

segments bright ferrugineus with the head slightly darker. Elytra deep black with the humeri and base piceus and the apices narrowly flavate. Apical two-thirds of fifth tergite black. Antennae and mouth parts ferrugineus. Legs pale flavate with the apices of the femora and the bases of the tibiae piceus, tarsi ferrugineus. Beneath largely ferrugineus with the mesasternum and metasternum piceus, apical half of fifth and most of sixth sternites black, the narrow apex of the latter flavate.

Head. — Head three-fifths as wide as long, widest across the eyes, the posterior margins of which are a little less than half the distance from the apex to the base; subparallel in anterior half, thence, rapidly narrowed to a cylindrical neck which is about one-fifth the length and one-fourth the width of the head. Anterior margin of head straight. Supra-antennal ridge prominent. Eye prominent, one-fifth the length of head. Antenna three-fifths longer than head, densely pubescent from the third segment, first segment as long as next six together, second segment twice as long as wide, narrower than apex of first, third through fifth segments each about two and one-half times as long as wide, about as wide as second, sixth through tenth segments each slightly shorter and just perceptibly wider than the preceding so that the tenth is only about one-fifth longer than wide, eleventh about as long as wide, pointed in apical third. Upper surface of head shining, with barely perceptible reticulate ground sculpture, finely, evenly, sparsely punctured throughout with a fine short pubescence interspersed with less numerous longer setae; at the base of each antennal ridge with a prominent fovea between which is a slight cntral impression, otherwise evenly convex. Each side of head behind the eyes with two large umbilicate punctures, the first on the upper surface one-third of the length of the eye from it, the other on the lower surface about the length of the eye from it. Under surface of the head impunctate except for about two dozen scattered fine punctures bearing fine long setae. Gular sutures widely separated in front, rapidly converging and thence very narrowly but distinctly separate to the neck where they diverge slightly. Maxillary palpus four-segmented, the first segment short, second long and slender, slightly arcuate, widest at apex, third slightly longer than second, hardly wider, widest at apex, almost straight, fourth segment semi-membranous, almost as wide at base as apex of third, almost as long as wide, conical with apex rather abruptly acuminate and membranous. Labial palpus three-segmented, first segment about twice as long as wide, second segment about as wide but half again as long as first, third segment about as long as first, acicular. Mandibles

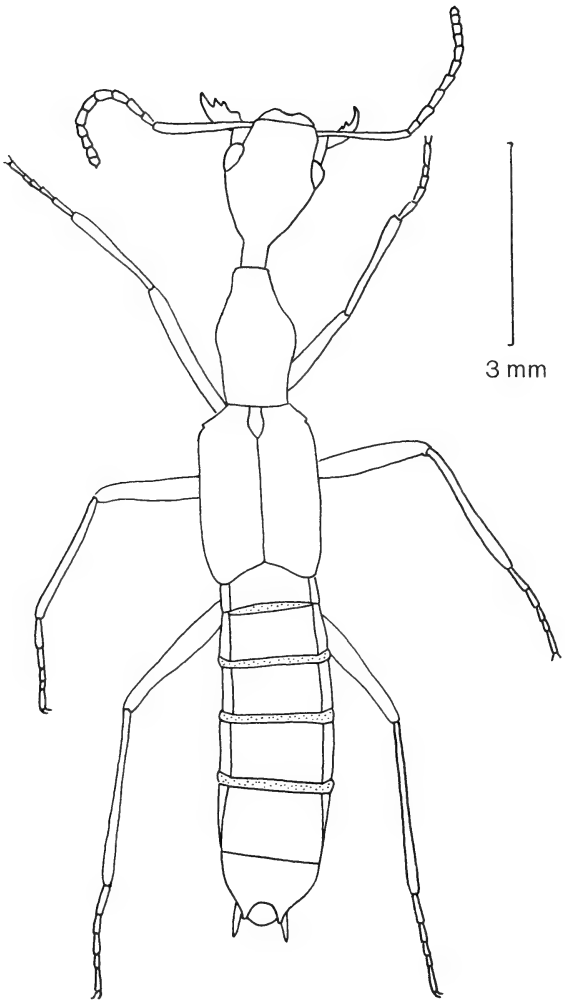


Figure 1. *Opithes crandalli* Moore, dorsal view.

long, slender, falcate, each with two large internal teeth, those of the left of nearly equal size, those of the right with the proximal tooth smallest.

Thorax. — Pronotum four-fifths as long as head, a little less than half as wide as long, widest near the middle, rapidly constricted to the front where it is about twice as wide as neck, rounded at the middle and narrowed posteriorly for a short distance, then straight and nearly parallel to the narrowly rounded basal angles; base straight, about one-fifth narrower than widest point; surface evenly convex, highly polished, impunctate on disc with large scattered umbilicate punctures along the base and for a short distance forward along each side. Superior lateral line short, about half the length of the pronotum, evanescent at each end. Prosternum longitudinally carinate with a few fine scattered setae. Lateral prosternal carina obliterated. Mesosternum narrow, not produced between the coxae. Metasternum long, broad, with an impressed longitudinal central line, very finely, very sparsely pubescent. Elytra hardly wider than head, conjointly almost one and one-half times as long as wide, humerus obtusely angulate with a minute tooth at the angle, sides nearly straight and nearly parallel, outer apical angles rounded, apices oblique, inner apical angles obtuse, sutures elevated, disc with six or seven irregular rows of crowded coarse punctures, interspaces shining. Legs very long and slender, anterior tarsus not dilated, without dense spatulate setae beneath. First segment of posterior tarsus longer than last segment, segments two, three and four decreasing in length.

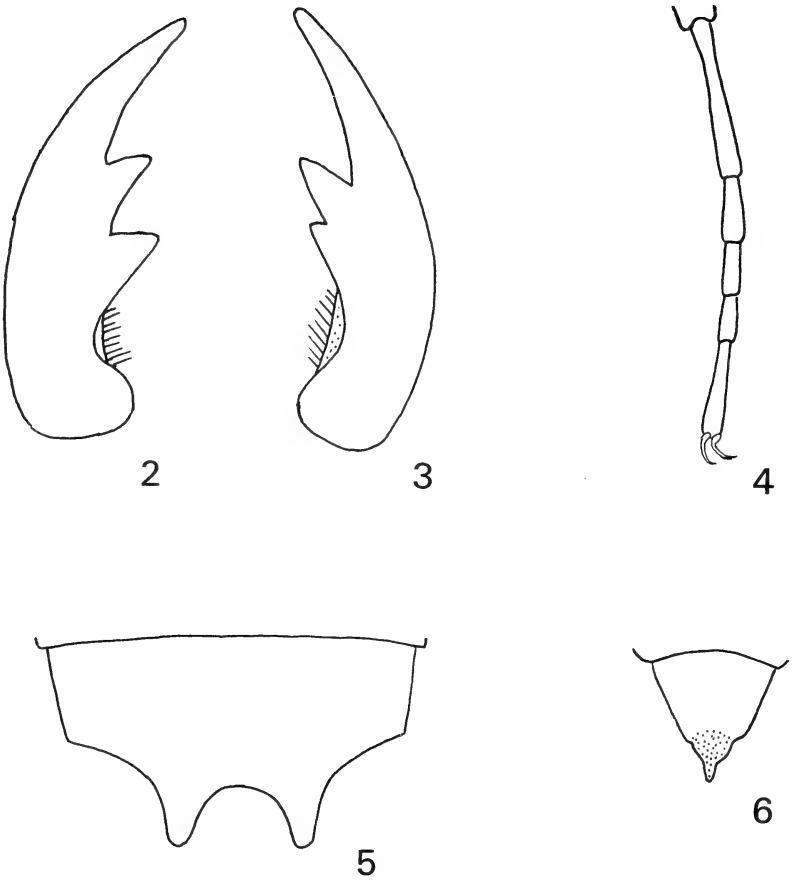
Abdomen. — Parallel, finely, sparsely, punctured, the punctures set with fine black setae with a few scattered larger setae particularly along the posterior margin. Last two segments somewhat more densely punctured than the others. Apical margin of sixth tergite about one-third of distance on each side produced in a large blunt tooth, the margin between the teeth broadly evenly arcuately emarginate. Vestiture beneath similar to above. Apex of sixth sternite arcuate with a very slight emargination in the central eight.

Length. — 12 mm.

Sex unknown but probably a female because of the condition of the sixth sternite, other species in the male have a deep incision in the apex of that sclerite.

Mexico, Sinaloa, Mazatlán, December 1966, R. H. Crandall, Jr., collector.

Disposition of type. — California Academy of Sciences, San Francisco.



Figures 2-6. *Opithes crandalli* Moore. 2, left mandible; 3. right mandible; 4, posterior tarsus; 5, sixth tergite; 6, fourth segment of maxillary palpus.

Notes. — This species is very similar in color to *fauveli* Lynch-Arribálzaga from Argentina but is without the central fovea on the disc of the head and has the abdomen more regularly marked without splotches of black.

This striking species is named for its collector, R. H. Crandall, Jr., who with his father has added many fine specimens to our collection.

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PSYCHE

Vol. 81 September-December, 1974 No. 3-4

HOST-PLANT UTILIZATION BY *PIERIS NAPI* POPULATIONS IN CALIFORNIA (LEPIDOPTERA: PIERIDAE)

By Arthur M. Shapiro[1]
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Oligophagous or polyphagous insects frequently exhibit ecologically or geographically complex patterns of host-plant utilization. Such patterns have recently been documented for the butterflies *Colias alexandra* Edwards (Pieridae) (Ellis, 1974) and *Euphydryas editha* Boisduval (Nymphalidae) (White and Singer, 1974). This paper reports a similar situation among California populations of the Gray-Veined White, *Pieris napi* Linnaeus (Pieridae) and notes its potential significance in interspecific competition.

Pieris napi is a circumpolar species; in its extensive boreal and temperate range it has been recorded on a great variety of plants of the family Cruciferae. In California it is widely distributed in foothill and lower montane (Yellow Pine-Incense Cedar-Douglas Fir) environments in the Coast Ranges south to San Luis Obispo County and in the Sierra Nevada at least as far south as Yosemite, but its host preferences have been very poorly documented. In their survey of Yosemite butterflies, Garth and Tilden (1963) listed in an Appendix "some plants on which Yosemite butterflies feed as larvae." Unfortunately these records, which are mostly not attributed, do not appear to be limited to Yosemite populations. Garth and Tilden list four Crucifer genera as hosts of *P. napi: Barbarea* (winter cress, yellow rocket), *Brassica* (mustard), *Raphanus* (radish), and *Dentaria* (milkmaids, crinkleroot, toothwort). Of these, all but *Raphanus* are known hosts of *P. napi* in the northeastern United States. Tilden (1965) recorded *P. napi* in the "San Francisco Bay area" on *Dentaria* only.

[1]This research was financed in part by grant D-804 from the Committee on Research of the Academic Senate, U.C. Davis.
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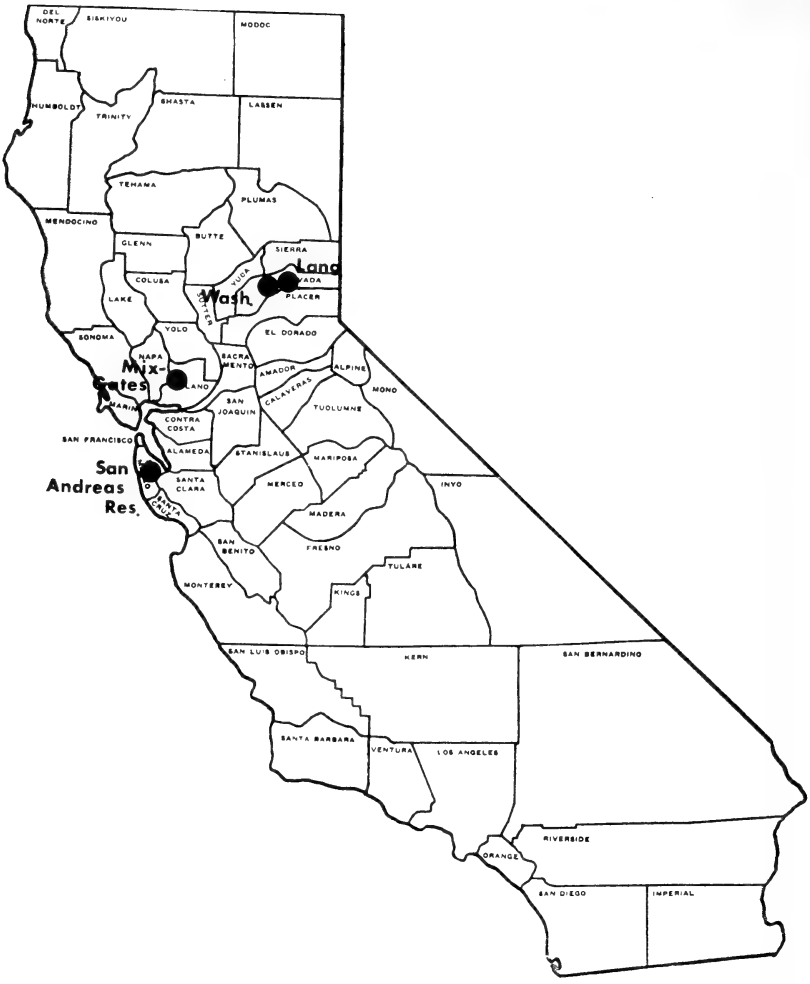

Figure 1. Locations of California *Pieris napi* populations.

During 1974 a number of Sierran and Coast Range populations of *P. napi* were sampled for photoperiodism studies, resulting in the incidental accumulation of data on host selection. The locations of these populations are shown in figure 1. The pattern of host selection proved to be of considerable interest, as reported below.

San Andreas Reservoir, San Mateo County. — This is a coastal, facultatively bivoltine population from a gully (elevation about 200 feet) subject to summer fog. On 10 April 1974, 58 ova of *P. napi* were found by searching 86 plants of *Barbarea verna* (Mill.) Asch., and three females were observed ovipositing on this plant. No ova were found on 25 plants of *Dentaria californica* Nutt. growing nearby in the same canyon. Ova on *B. verna* were placed on leaves (mostly on lower surfaces), stems, and pedicels. Most of the *Barbarea* plants had only cauline leaves and were in the early stages of flowering. *Dentaria* were in the advanced stages of flowering and had some green siliques.

Mix and Gates Canyons, Solano County. — This is a strictly univoltine population from summer-arid canyons of the east slope of the Vaca Mountains, central Inner Coast Ranges, open to the Sacramento Valley (elevations 500 to 2000 feet). On 4 April 1974, 39 ova of *P. napi* and 21 of *Anthocaris sara* Reakirt were found on 66 plants of *Barbarea verna;* the *sara* ova were mostly in the inflorescence and on the upper surfaces of leaves, while the *napi* ova were scattered as described for San Mateo County, but seldom on the upper surfaces of leaves. No Pierid ova of any kind were found on 40 *Dentaria californica* near the *Barbarea.* On 19 May 1974, 14 larvae of *P. napi* were collected on *B. verna.* They were feeding on leaves, and the green siliques had not been damaged although most of the plants were nearly or quite defoliated; only one *napi* larva was found feeding on siliques, and this was on a plant whose leaves and petioles had been entirely consumed. Seven larvae of *A. sara* were found on five plants of *Sisymbrium officinale* (L.) Scop. (hedge mustard) and two on *B. verna.* All of these were feeding on green siliques only, on plants whose leaves were undamaged. Four of 20 *Dentaria* examined had been defoliated, apparently by Pierid larvae, but no larvae were collected.

Near Washington, Nevada County. — Located in the South Yuba River canyon at about 2600 feet on the west slope of the Sierra, this is also a univoltine population. On 3 May 1974, 78 ova of *P. napi* were collected by the author and S. R. Sims from about two dozen immature *Arabis glabra* (L.) Bernh. (tower mustard). The ova

had been laid on both upper and lower surfaces of rosette leaves, lower surfaces of the (appressed) cauline leaves (often near the point of attachment, as was also true on *Barbarea verna*), and on stems. One larva (3rd instar) was found, and two ovipositing females were observed. On 22 May, 16 additional ova and 5 larvae were found at the same spot on the same plants, which were now mature and beginning to set fruit. Abundant evidence of larval feeding was found on the rosettes and lower cauline leaves, but the flowers and siliques were undamaged. Fourteen plants of flowering *Barbarea orthoceras* Ledeb. were found in a grassy meadow 0.7 mile up the canyon, within the area where adult *P. napi* had been seen, but no ova, larvae, or feeding damage could be located on them.

Lang Crossing, Nevada County. — This population is at about 4500 feet in the South Yuba River canyon, at or near the upper altidudinal limit of Sierran *P. napi;* it is also univoltine. On 22 May 1974, 3 ova of *P. napi* were found in a stand of 30 immature *Arabis glabra* and none on 20 flowering *Barbarea orthoceras* growing immediately adjacent to them. On 2 June the same stand was again searched, producing 11 ova of *P. napi,* 20 of *P. rapae* Linnaeus, 3 of *A. sara* and 2 of *Anthocaris lanceolata* Lucas from *A. glabra,* and 8 of *A. sara* from *B. orthoceras.* An additional 34 ova of *P. napi* were collected from *A. glabra* elsewhere in the vicinity. Four larvae of *P. napi* were found feeding on rosette leaves of *A. glabra,* and two of *A. sara* on inflorescences and siliques of *B. orthoceras.* On 26 June four mature *A. sara* and two immature *A. lanceolata* larvae were found on siliques of *A. glabra* and one mature *A. sara* larva on siliques of *B. orthoceras.* Many *A. glabra* plants showed feeding damage to the rosettes, but only seven *P. rapae* larvae were found; probably most *napi* had already pupated. *Pieris rapae,* which is multivoltine, was flying in abundance at Lang Crossing on 19 July.

Despite the large number of Pierid species and individuals, the visible impact of feeding on the Crucifers at Lang Crossing was quite small. In particular, *Arabis glabra* plants often produced several hundred siliques on leafy, two- to four-foot stems.

Discussion

There are ten species of obligate Crucifer-feeding Pierids in California, occurring in various combinations at different localities. Some of these are spring-univoltine, a few are spring-bivoltine, and some are multivoltine. How they partition the available Crucifers among themselves may shed valuable light on the broad problems

of niche differentiation, competitive exclusion, and species packing. Emmel (1974) reported three species of inflorescence feeders (*Pieris protodice* Boisduval and LeConte, *A. sara* and *A. lanceolata*) on *Arabis glabra* in Riverside County, 2 June 1973. Shapiro (1974) described five- and six-species Pierid assemblages in two high Sierran localities and concluded that competition is reduced by behavioral mechanisms (habitat selection).

Pieris napi occurs with up to six other Crucifer-feeding Pierids at the four localities described above. Based on adult collections, the Crucifer-feeding Pierid faunas of the four localities are (inflorescence feeders are marked "I"; others primarily leaf feeders):

San Andreas Reservoir: *P. napi, P. rapae, A. sara* (I), *Euchloe ausonides* Lucas (I).

Mix and Gates Canyons: *P. napi, P. rapae, P. sisymbrii* Boisduval (I?), *A. sara* (I), *E. ausonides* (I).

Washington: *P. napi, P. rapae, A. sara* (I), *A. lanceolata* (I), *E. ausonides* (I).

Lang Crossing: *P. napi, P. rapae, P. sisymbrii* (I?), *A. sara* (I), *A. lanceolata* (I), *E. ausonides* (I), *E. hyantis* Edwards (I).

Not all of these breed in the same microhabitats. At Lang Crossing, for example, *P. sisymbrii* and *E. hyantis* are found only in exposed rocky situations and appear to breed only on *Streptanthus,* and are thus not in competition with the woodland species. In examining the fauna of particular plants in particular habitats, the division of Pierids into a leaf-feeding and an inflorescence/silique feeding guild seems paramount. At Mix and Gates Canyons, where *Barbarea* is obviously in "short supply" and frequently completely defoliated, at least one species from each guild (*P. napi, A. sara*) can occur on this plant. At Lang Crossing the combined visible impact of four species — two of each guild — on *Arabis glabra* is so small that it is tempting to speculate that the populations are regulated by other factors below the level at which interspecific competition would be significant.

Despite the potential for interspecific competition, at each of the study areas one plant received the bulk of the attention from Pierids while another appeared largely or wholly unutilized. It remains to be seen whether this reflects nutritional or toxicological unsuitability of certain Crucifer species. (In unpublished laboratory studies, Shapiro and F. Slansky (*pers. comm.*) have found variation in the suitability of native and weedy Crucifers as hosts of *Pieris rapae*

and other species.) It is also possible that host selection by ovipositing females is closely tied to host plant phenology, and that flowering condition of the plants, and possible correlated changes in mustard oil concentrations, may determine the patterns observed.

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NEW *PROTONEMURA* (S. L.) FROM NEPAL (PLECOPTERA; NEMOURIDAE)*

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Described below are the stoneflies of the genus *Protonemura* (Nemouridae) collected in 1967 by the Canadian Nepal Expedition organized by the Entomological Research Institute of the Canada Department of Agriculture in Ottawa. The genus *Protonemura* is understood here in its widest sense (sensu lato) as used by Kimmins (1946, 1950) and Aubert (1967); the genus is obviously in need of a revision as it contains a wide assemblage of forms some of which bear larval gills and some which do not. The species considered here are apparently gill-less as far as can be ascertained from the adults.

The material examined comes from six localities: Godavari at altitudes of 5000 ft and 6000 ft, Bhurunche at an altitude of 8500-9500 ft, and four localities known only from their geographical coordinates and altitudes: 27°56′N, 85°00′E at 9900 ft and 10100 ft, 27°57′N, 84°59′E at 10100 ft, 27°58′N, 85°00′ E at 11100 ft, and 28°00′N, 85°00′E at 9900 ft. Most of the specimens were collected in Malaise traps and therefore the collection dates indicate the period between visits to the traps.

All the specimens are preserved in alcohol and are deposited in the Canadian National Collection of Insects in Ottawa. The drawings have been prepared from cleared specimens. Only the species represented by male specimens have been named, the others have been designated by letters to prevent useless future synonymy.

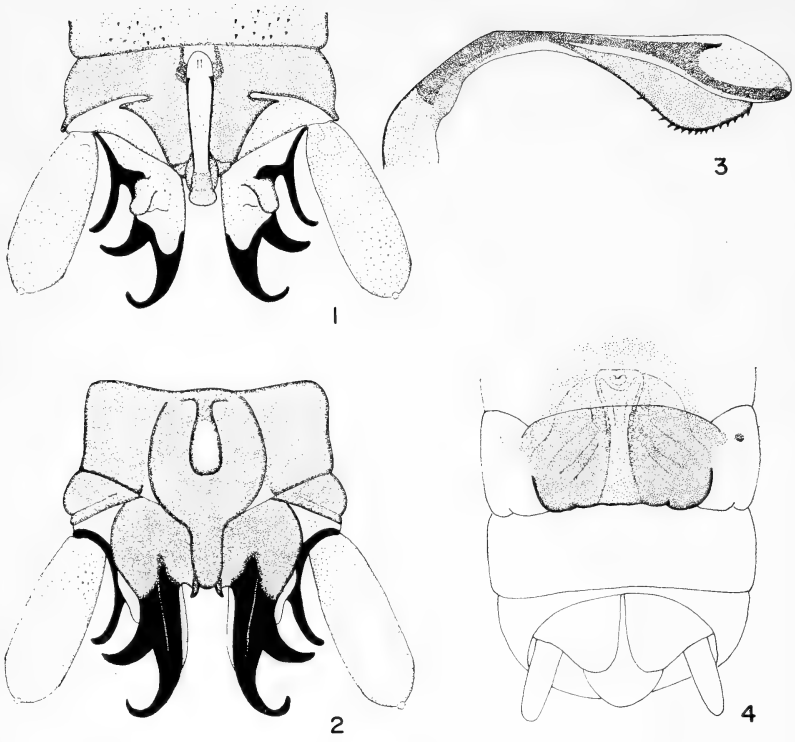
Protonemura mira, n. sp.

Figures 1-4

Length of body 11 (♂)-14 (♀) mm, to tips of wings 16 (♂)-19 (♀) mm.

General coloration dark reddish brown; antennae black; anterior and lateral margins of pronotum light; wings uniformly brown; legs brown, tarsi and distal end of femora darkened; metafemora also with a subapical dark ring. Abdomen mostly membranous except for the genital segments and a pair of sclerotized tergal plates on each segment in the male. Genitalia reddish brown.

Manuscript received by the editor November 18, 1974.



Figures 1-4: *Protonemura mira* Harper, n. sp. 1. Terminal segments of male with paraprocts slightly pulled out (dorsal). 2. The same (ventral). 3. Epiproct (lateral). 4. Terminal segments of female (ventral).

Male genitalia: median lobe of sternum IX long and narrow, ventral vesicle short. Paraproct: median lamella small, slightly curved, extending just beyond sternum IX; subanal plate wide, its process forming two dark heavy hooks; subanal vesicle short; external appendage finger-like, heavily sclerotized and gradually curved. Cerci long and membranous. Tergum IX with a few spinules on its posterior margin. Epiproct long and slender with an expanded tip bearing a double row of ventral spinules.

Female genitalia: subgenital plate sclerotized, wide, with rounded corners, but not produced posteriorly. Vaginal structures as in Figure 4, somewhat reminiscent of *Protonemura* A of Aubert (1967, Fig. 99), but the subgenital plates are different.

Holotype: ♂, Godavari, 6000 ft, 17-20. VII. 1967 (CNC type no. 13430). Allotype: ♀, and paratype: ♀, same data.

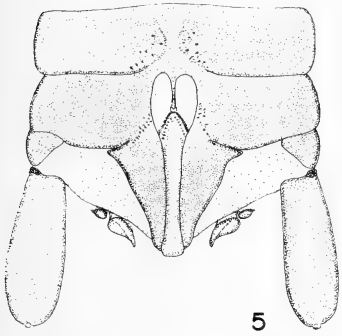
Diagnosis: P. mira clearly belongs to the *P. indica* Kimmins group as defined by Aubert (1967); the shape of the process of the paraprocts of the male and the subgenital plate as well as the vaginal structures of the female will easily separate *mira* from the other known species of the group.

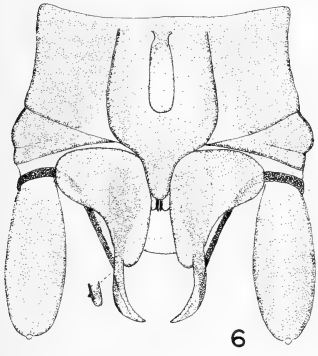
Protonemura godavariensis, n. sp.

Figures 5-8

Length of body 10-13 mm, to tips of wings 13-15 mm.

General coloration dark brown. Wings uniformly brown. Legs brownish, femora with two subapical dark bands. Abdomen brownish, genitalia dark brown.





Figures 5-8: *Protonemura godavariensis* Harper, n. sp. 5. Terminal segments of male (dorsal). 6. The same (ventral). 7. Epiproct (lateral). 8. Terminal segments of female (ventral).

Male genitalia: median lobe of sternum IX narrow and of moderate length; ventral vesicle reaching beyond middle of sternum. Paraproct: median lamella short and pointed, heavily sclerotized; subanal plate wide, triangular, with broadly rounded angles; distal process forming a long curved trough-like appendage; external appendage finger-like, heavily sclerotized externally and bearing a subapical lateral tooth; the external appendage extends just beyond the subanal plate. Cerci long and membranous. Terga IX and X bearing small fields of spinules. Epiproct long and slender, its tip expanded laterally and bearing ventrally a short double row of heavy teeth.

Female genitalia: subgenital plate well sclerotized, prolonged posteriorly into a trapezoidal lobe which is broadly and regularly emarginate. Vaginal structures as in Figure 8.

Holotype: ♂, Godavari, 5000 ft, 20-23.VII.1967 (CNC type no. 13431); allotype: ♀, same data; paratypes: ♂, ♀, same locality, 20.VII.-4.VIII. 1967.

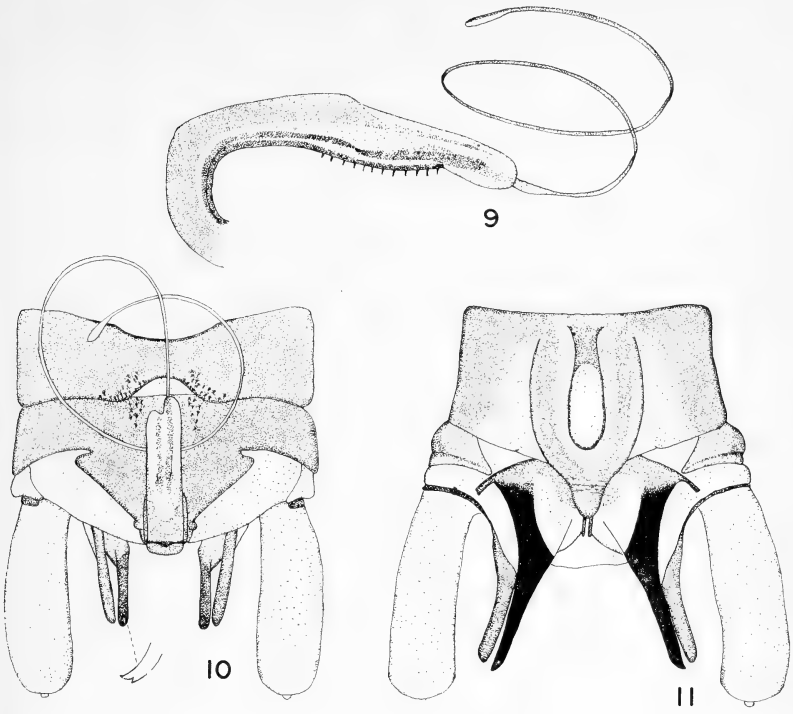
Diagnosis: as the preceding species, *P. godavariensis* belongs to the *P. indica* group. The trough-like process of the subanal lobe of the male as well as the vaginal structures of the female are good diagnostic characters. The species is very close to *P. assami* Aubert and may eventually prove to be the same.

Protonemura funicula, n. sp.
Figures 9-11

Length of body, 11-12 mm, to tips of wings, 18-19 mm.

General coloration brown; head and disk of pronotum dark brown. Wings clear, veins of the front wings marginated with brown. Legs banded: femora with a median and distal dark band, tibiae narrowly darkened at base and darkened again distally, tarsi dark. Abdomen mostly membranous except the genital segments; in the male a pair of small ventral sclerites and a pair of larger dorsal sclerites are borne at the base of each abdominal segment.

Male genitalia: sternum IX long with a short rounded median lobe; ventral vesicle large reaching three quarters of the length of the sternum. Paraproct: median lamella narrow; subanal plate partly membranous, irregularly triangular, prolonged distally into a heavily sclerotized process which is slightly recurved dorsally; this process is pointed apically and bears a sharp subterminal spine; ex-



Figures 9-11: *Protonemura funicula* Harper, n. sp. 9. Epiproct (lateral). 10. Terminal segments of male (dorsal). 11. The same (ventral).

ternal appendage moderately sclerotized, finger-like, and reaching out as far as the process. Cerci long and membranous. Terga IX and X with small median fields of spinules. Epiproct narrow and flat, asymmetrical distally and prolonged by a very long whip-like process.

Female: unknown.

Holotype: ♂, 27°57′N, 84°59′E, 10100 ft, 26-31.V.1967 (CNC type no. 13432); paratypes: ♂, 27°56′N, 85°00′E, 10100 ft, 23-29. V.1967; ♂, 27°58′N, 85°00′E, 11100 ft, 25.V.1967; 3♂, 28°00′N, 85°00′E, 9900 ft, 27.V.-22.VI.1967.

Diagnosis: P. funicula can be placed in the *P. filigera* (Kimmins) group of Aubert (1967). The shape of the subanal lobes and the particularly long appendage of the epiproct are distinctive.

Protonemura adunca, n. sp.
Figures 12-14

Length of body 10-11 mm, to tips of wings, 13-14 mm.

General coloration dark brown; antennae and disk of pronotum nearly black. Wings amber, veins darker. Legs particularly the hind pair banded; femora with a median and a distal band. Abdomen membranous except the genital segments; in the male there is also a pair of small sclerites at the base of each tergum.

Male genitalia: sternum IX broadly pentagonal, prolonged into a long and tapering median lobe; this median lobe bears distally an apical expansion which is outturned at a right angle from the lobe and forms a beak-like extension ending in two sharp points. Paraproct: median lamella narrow and rounded apically; subanal plate sclerotized at base, divided distally into three lobes, the inner lobe short and rounded, the intermediate lobe membranous, and the outer lobe long and digitiform, fused laterally with the external appendage; external appendage fused with subanal lobe for most of its length, terminating distally in a beak-like point. Cerci long, membranous, and expanded slightly at tips. Tergum IX emarginate centrally, the emargination bearing short spinules. Tergum X excavated anteriorly, and prolonged into two short median lobes covered with spinules. Epiproct cylindrical, asymmetrical beyond middle, and terminating in a short curved lobe; a short irregular group of spinules at base of epiproct.

Female: unknown.

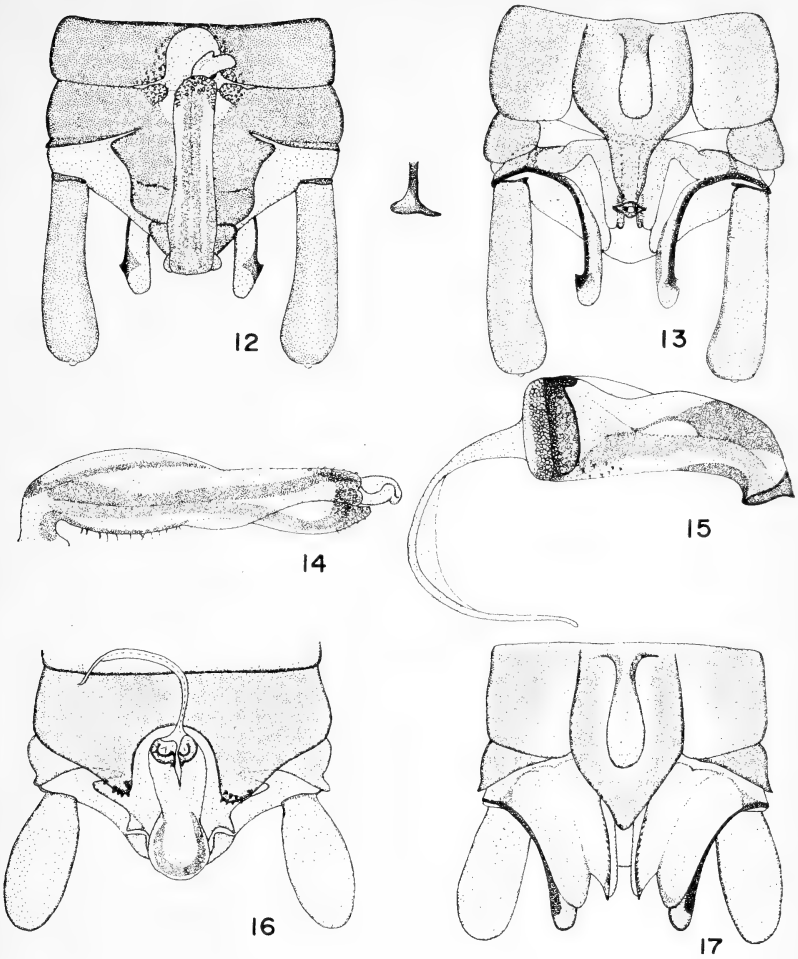
Holotype: ♂, 27°57′N, 84°59′E, 10100 ft, 26-31.V.1967, (CNC type no. 13433); paratypes: ♂, same data; ♂, 27°58′N, 85°00′E, 11100 ft, 18.V.1967; 4♂, 28°00′N, 85°00′E, 9900 ft, 21.V.-22.VI. 1967; 2♂, Bhurunche, 8500-9500 ft, 23.V.1967.

Diagnosis: P. adunca probably fits into the *P. filigera* group on the basis of its epiproct. The shape of the distal end of the median lobe of sternum IX is quite distinctive and unique.

Protonemura mastigophora, n. sp.
Figures 15-17

Length of body 10 mm, to tips of wings, 13 mm.

General coloration dark brown. Head nearly black (antennae missing). Wings brownish with some darker clouds. Legs banded, particularly the hind pair; femora with a dark distal band and a paler median one. Abdomen membranous except for the genital segments.



Figures 12-14: *Protonemura adunca* Harper, n. sp. 12. Terminal segments of male (dorsal). 13. The same (ventral). Figures 15-17: *Protonemura mastigophora* Harper, n. sp. 15. Epiproct (lateral). 16. Terminal segments of male (dorsal). 17. The same (ventral).

Male genitalia: sternum IX long and pentagonal; median lobe short and inconspicuous; ventral vesicle large. Paraproct: median lamella long, thin, and extending backwards as far as the subanal plate; subanal plate terminating in two finger-like lobes, a shorter median lobe, and a larger lateral lobe; external appendage fused to lateral lobe of subanal plate and extending three quarters of its length. Tergum IX produced posteriorly into two asymmetrical lobes separated by a large median excavation; each lobe bears a distal patch of spines. Tergum X normal. Epiproct short and stocky, remarkably asymmetrical, and bearing a terminal whip-like appendage.

Female: unknown.

Holotype: ♂, 27°56′N, 85°00′E, 10100 ft, 23-29.V.1967 (CNC type no. 13493).

Diagnosis: another member of the *P. filigera* group, *P. mastigophora* is close to the species *filigera* (Kimmins 1946), *parafiligera* Aubert 1967 and *metafiligera* Aubert 1967. It can be best distinguished from the others by the shape and the sclerotizations of its epiproct; these are not as well produced in *P. filigera* the species it resembles most; Kimmins' (1946) drawing shows no detail of the inner structure of the epiproct, but a specimen in the United States National Museum (det. R. W. Baumann) does not possess the structures described here for *mastigophora.*

Protonemura A
Figure 18

In general structure and coloration, this female agrees with *P. funicula* and *P. adunca;* it could be the female of either.

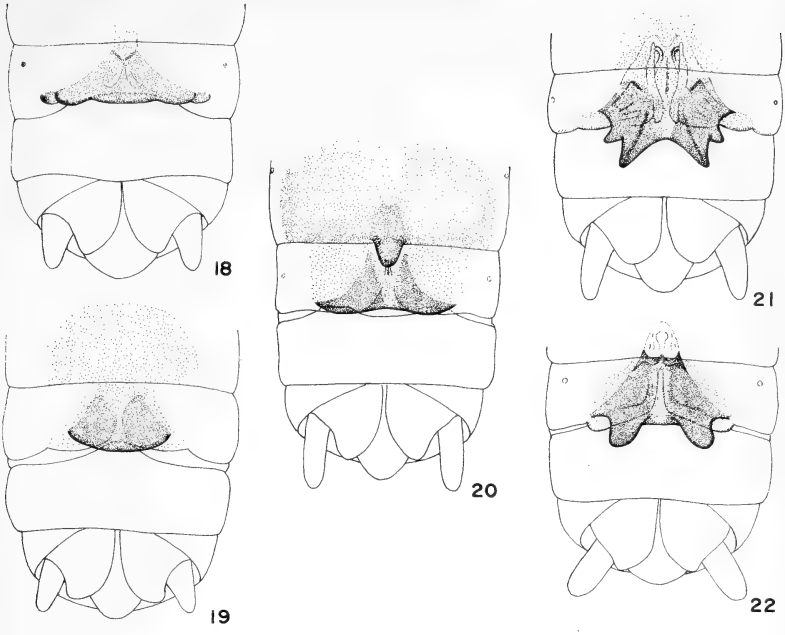
Female genitalia: the subgenital plate is very slightly trilobed. Vaginal structures as in Figure 18.

Material examined: ♀, 27°56′N, 85°00′E, 9900 ft, 23-29.V.1967; 6♀, 27°57′N, 84°59′E, 10100 ft, 19-31.V.1967; 5♀, 27°58′N, 85°00′E, 11100 ft, 8-24.VI.1967; 4♀, 28°00′N, 85°00′E, 9900 ft, 14.V.-22.VI.1967.

Protonemura B
Figure 19

Total length 10 mm, to tips of wings, 13 mm.

General coloration brown. Wings uniformly amber. Legs banded in the usual manner.



Figures 18-22: Terminal segments of unassociated females (ventral). 18. *Protonemura* A. 19. *Protonemura* B. 20. *Protonemura* C. 21. *Protonemura* D. 22. *Protonemura* E.

Female genitalia: subgenital plate small, and rounded posteriorly. Sternum VII sclerotized medially. Vaginal structures indistinct.

Material examined: ♀, 28°00′N, 85°00′E, 9900 ft, 27.V.-22.VI. 1967.

Protonemura C
Figure 20

Total length 11-12 mm, to tips of wings, 15-16 mm.

General coloration brown. Wings yellowish-brown, veins dark brown, marginated with brown. Legs brown with a subterminal white band.

Female genitalia: subgenital plate short, slightly bilobed. Sternum VII heavily sclerotized bearing an important posterior nipple-like protuberance. Vaginal structures indistinct.

Material examined: 22♀, 27°58′N, 85°00′E, 11100 ft, 2-24.VI. 1967.

Protonemura D
Figure 21

Total length 15 mm, to tips of wings, 18 mm.

General coloration dark brown. Wings blackish. Pro- and meso-femora light brown with an apical darkening, meta-femora brown with a subapical light ring.

Female genitalia: sternum VII lightly sclerotized medially. Subgenital plate forming posteriorly two pairs of lobes separated by a wide emargination. Vaginal structures very characteristic, as in Figure 21.

Material examined: 2 ♀, Godavari, 6000 ft, 14-20.VII.1967.

Remarks: This species evidently belongs to the *P. indica* group; it can be separated from *P. indica* Kimmins 1946 and *P. quadridentata* Kimmins 1950 (see Figures 18, 29 & 30 in Aubert 1967) the species it resembles most by the shape of its vaginal structures and by its medially pigmented (and sclerotized) seventh sternum.

Protonemura E
Figure 22

Total length 13 mm, to tips of wings, 16 mm.

General coloration similar to that of *Protonemura* D.

Female genitalia: subgenital plate produced into two rounded posterolateral lobes. Vaginal structures very distinctive, as in Figure 22.

Material examined: ♀, Godavari, 6000 ft, 17-20.VII.1967.

Acknowledgments

I thank Mr. J. E. H. Martin of the Canada Department of Agriculture in Ottawa for allowing me to study this material and Dr. R. W. Baumann of the United States National Museum for the loan of material and the comparison of specimens.

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THE EYELESS *CATOPOCERUS* BEETLES (LEIODIDAE) OF EASTERN NORTH AMRICA*

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The Leiodid beetle genus *Catopocerus* Motschoulsky 1869 is composed exclusively of small (1.8-4.5 mm body length), eyeless, wingless, partially depigmented inhabitants of moist forest soil and duff, and occasionally of caves. The genus, the only member of the subfamily Catopocerinae, is known to occur only in North America. The distribution of the genus is principally the unglaciated mountain forests of the eastern and western portions of the continent.

Hatch (1957) has reviewed the nine described species from western North America. These range from the San Francisco area northward in coastal forests to Sitka, Alaska. Undescribed species occur in this region and also in southern California, Arizona, and Colorado (personal data). The known and new western species will be covered in a future paper which will also include data from an assemblage of over 2000 specimens collected throughout Oregon by Ellen Benedict of Portland State University.

This paper reports on the two described eastern North American species, and describes three new eastern species.

The genus possesses a character common to the family; the eighth antennal segment is smaller than either the seventh or ninth segments (except in *C. pusio* Horn of California in which the seventh and eighth segments are equally small). They may be distinguished from other leiodids by a combination of the following characters: eyelessness, winglessness, oval shape, dorsal-ventral flattening, open procoxal cavities, five segmented abdomen, and separated metacoxae (Peck, 1973:50).

Methods

In the field, series of specimens were taken from moist forest litter, soil, and well-rotted logs. The debris was sifted in the field through a one-half inch mesh screen to remove large objects. The sifted debris was carried and stored in large plastic bags until it could be processed in "Berlese" funnels. When processed, three liters of litter were placed in each funnel (45 cm high, 30 cm across the top, with the

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screen 10 cm from the top) on a double layer of cheesecloth supported by the screen. A 40 watt bulb was used over the litter. Two thin wood strips held the top of the funnel above the rim of the bottom and provided ventilation and for the escape of excess moisture. Beetles stopped falling into the collecting bottle at the bottom of the funnel in less than 12 hours. During periods of maximum operation, up to 24 funnels were used, each holding three liter samples of sifted litter for twelve hours. Thus, up to 144 liters of sifted litter could be processed each day.

From 1967 to 1974, in search of *Catopocerus* and other leiodid beetles, I have extracted the fauna in the above method from 4361 kg of sifted forest litter from the eastern United States. Most of the beetles extracted have been deposited with the CNCI and FMNH, and the arthropod residues are in the FMNH.

Barber's Fluid (Valentine, 1942) was used as a preservative under the funnels. Species determination can be reliably made only by examination of the male genitalia. This examination is facilitated by the Barber's Fluid which does not harden the tissues of the beetles as does alcohol. The few specimens found under rocks were collected into Barber's Fluid. Some specimens were collected in caves at rotted pig liver bait, and in carrion baited pitfall traps (Peck, 1973). Specimens were cleaned of adhering debris by an ultrasonic cleaner. Dry material was relaxed in boiling water. Dissections were made with minuten needles, in alcohol. Genitalia were observed in alcohol, as temporary glycerine mounts, and dry. Specimens were mounted on points using an alcohol soluble glue. Illustrations were prepared from temporary glycerine mounts.

Measurements are given in millimeters, and were made using a calibrated ocular micrometer disc. The following abbreviations are used in the paper: HW, head width; PW, pronotal width; PL, pronotal length; EL, elytral length; and EW, elytral width. Lengths were measured along the midline. Elytral lengths are from the apex of the scutellum. Widths are maximum widths. Rounded surfaces are measured as chords of arcs.

The following abbreviations are used to indicate the sources of the material examined: AMNH, American Museum of Natural History; ANSP, Academy Natural Sciences Philadelphia (Horn colln., now in MCZ); CAS, California Academy of Sciences; CM, Carnegie Museum; CNCI, Canadian National Collection of Insects; FMNH, Field Museum of Natural History; INHS, Illinois Natural History Survey; MCZ, Museum Comparative Zoology, Harvard University; SBP, Stewart B. Peck; SVAM, St. Vincent Archabbey Museum

Collection, Latrobe, Penn.; UK, University of Kansas, Entomology Collection; USNM, United States National Museum.

Bionomics

The general collector may occasionally encounter *Catopocerus* under large rocks and logs in mountain forests. Large series are most usually taken in the spring and fall and only by extraction from soil and litter with the Tullgren modification of a Berlese funnel. Some species have been found in caves in the eastern interior low plateaus. Here they are usually under rocks in organic soil near cave entrances. The use of carrion bait has been useful in attracting the beetles in caves.

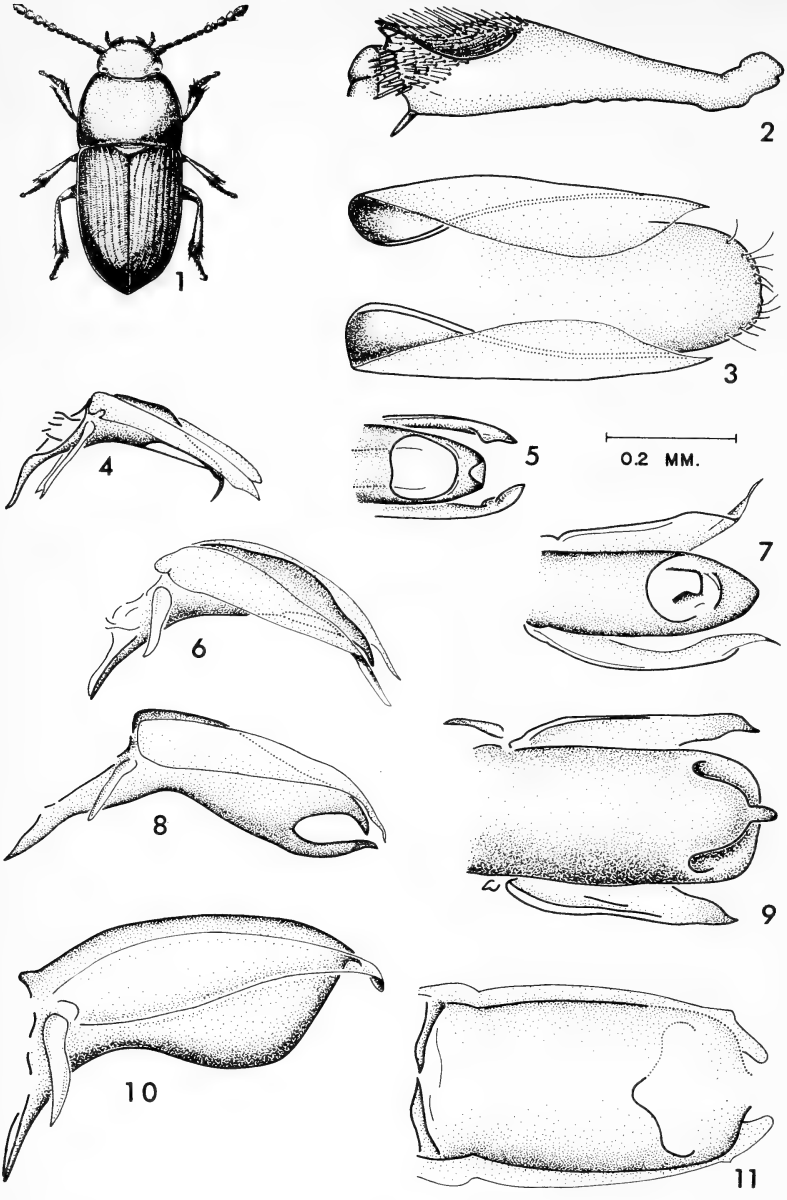
Food probably consists of organic debris and associated yeasts and fungi. Several species of *Catopocerus* have been repeatedly taken on subterranean fungi in Oregon and Washington (Fogel and Peck, in MS) and the eastern species may have similar habits. A laboratory colony of the beetles reproduced and developed on bakers yeast on moist soil. *C. hamiltoni* was taken congregated around a dead beetle larva, and the many beetles taken on carrion bait in caves were undoubtedly attracted to the carrion for the purposes of feeding and/or oviposition.

Only one certain case of sympathy is known. Thirty-four *C. ulkei* and 11 *C. appalachianus* were taken together in 10 kg of litter near Whitmer, W. Va.

Reproduction may occur throughout the year in caves, but in forest litter is probably most active in the spring. Larvae and teneral adults have been found most commonly in early spring in litter. One species has been reared from eggs. At 15°C, the egg stage lasts about 17 days, the larval stage about 29 days, and the pupal stage 20 days.

Three species have been found in caves in Alabama and Tennessee. However, this association with caves is only facultative, for these soil-inhabiting (edaphobitic) beetles probably accidentally enter caves, but once there can survive and reproduce.

One of these species, *C. appalachianus* is found at higher elevations in the Appalachians near the soil surface under rocks and in litter. If the preferred environment of the beetles is a montane type of stable, cool, and moist environment, this will be found at lower elevations deeper in the soil. Collecting of surface soil and litter has never taken the beetles at the lower elevations of the Cumberland Plateau or Highland Rim of Alabama or Tennessee. Thus, in the cave region, the beetles' normal soil habitat must be too deep to be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normally sampled, and this deep soil habitat will bring the beetles into frequent contact with rock crevices filled and partly filled with soil, which may open into caves with their cool and moist conditions. Hence, in the southern Appalachians, caves can be a more convenient sampling site for soil inhabitants which are usually hidden under a concealing thickness of soil. Other such montane soil inhabitants that are infrequently found at lower elevations except in caves are *Anillinus* carabids (Barr, 1969) and *Arianops* pselaphids (Barr, 1974). Collecting in prolonged wet weather or during winter months might find all of these beetles closer to the surface in the Cumberland Plateau or Highland Rim regions of Alabama and Tennessee.

Artificial key to the *Catopocerus*

1a. Body length 4mm or over ..... *C. hamiltoni*
1b. Body length 3mm or under 2
2a. Hind tibia with setal bearing excavation on dorsal posterior surface (fig. 2) ..... *C. alabamae,* n. sp.
2b. Hind tibia with setae only, no excavation on dorsal posterior surface 3
3a. Third antennal segment clearly longer than second, five clearly larger than four and six; northeastern Alabama *C. jonesi,* n. sp.
3b. Third antennal segment as long as or only slightly longer than the second, five the same size as four and six; widely distributed 4
4a. Tip of aedeagus curved downward, forming 80° to 100° angle with ventral surface of aedeagus (Fig. 4) ..... *C. ulkei*
4b. Tip of aedeagus only slightly curved downward, angle with ventral surface of aedeagus 135° or greater (Fig. 6) ..... *C. appalachianus,* n. sp.

Catopocerus hamiltoni (Horn)

Fig. 3; Map 2

Pinodytes hamiltoni Horn, 1892:45. Lectotype here designated as female in MCZ, Horn coll'n. (no. 3027), seen. Type locality: "vicinity of Allegheny City", Pennsylvania.

Figures 1-11. 1, habitus of *Catopocerus appalachianus.* 2, metatibia of *C. alabamae.* 3, aedeagus of *C. hamiltoni.* 4, side of aedeagus of *C. ulkei.* 5, ventral tip of aedeagus of *C. ulkei.* 6, side of aedeagus of *C. appalachianus.* 7, ventral tip of aedeagus of *C. appalachianus.* 8, side of aedeagus of *C. jonesi.* 9, ventral view of aedeagus of *C. jonesi.* 10, side of aedeagus of *C. alabamae.* 11, ventral view of aedeagus of *C. alabamae,* tip incomplete because of damage in dissection. Scale line for figs. 3-11 only.

Diagnosis. The large size, the third antennal segment which is 1.5 times or more the length of the second segment, and the shape of the aedeagus serve to distinguish this species.

Redescription. Measurement of lectotype: HW, 0.85. PW, 1.63. PL, 1.23. EW, 1.63. EL, 2.74.

Length 4.1-4.7 mm. Width 1.66-1.73 mm. Color uniform dark reddish-brown, shining. Shape oblong, moderately elongate, not very convex.

Head without trace of eyes; sparsely punctate. Antennae well supplied with long hairs throughout length, last three segments with dense vestiture; segment III 1.5× or more the length of II; III slightly wider than II; IV, V, VI as wide as II, subglobose, slightly longer than wide; VII, IX, X cup shaped; VII longer than but narrower than IX and X; VIII shorter than but slightly wider than VI; XI conical.

Pronotum widest at middle, sides evenly arcuate; narrower at front than back; hind angles rectangular; front angles rounded; front margin evenly emarginate to receive head; hind margin weakly convex; disc finely but not closely punctate; covered with fine strigae.

Elytra fused; at base slightly wider than base of pronotum; widest at middle; sides slightly arcuate; narrowing in apical third; each with seven striae of close punctures, less distinct at sides and apex, intervals flat, sparsely punctate.

Protibia gradually widening to apex; setose on apical half of inner margin. Mesotibia gradually widening to apex; sharply outward flaring in outer margin at apex; spinose on outer concave margin; inner margin sinuous; setose on apical half of inner margin. Metatibia gradually widening to apex; inner and outer margin slightly sinuous; setae on apical half of inner margin. Penultimate abdominal segment, fourth, with transverse depression on either side.

Male protarsomeres not dilated. Abdominal segment five truncate. Aedeagus poorly sclerotized; thin and straight in lateral view; wide and straight in dorsal view; tip dorsoventrally flattened, slightly upturned at edge, smoothly rounded in dorsal view, 14 setae along edge; parameres separated, longest on ventral surface but not reaching tip of aedeagus, partially covering anterior ventral surface and dorsal median surface of aedeagus (fig. 3).

Female abdominal segment five rounded.

Note on lectotype. The specimen is damaged. It possesses only two prothoracic and one metathoracic legs. One antenna is missing its terminal segments.

Distribution. Southwestern Pennsylvania (map 2). The type locality, Allegheny City, lying on the north shore of the confluence of the Allegheny and Monongahela Rivers, was incorporated into the city of Pittsburgh near the beginning of this century.

Material examined. Pennsylvania. Allegheny, 1 female, lectotype 3027 (ANSP); 2, (ANSP, CM). Beatty, 1 female (USNM). Charleroi, 2 (MCZ, UK). Jeannette, vi. 1901, 2 (CM). Pittsburgh, ix, 2 (CM). St. Vincent, 3 (Ulke colln. in CM; MCZ). Washington Co., 1 female (Fall colln. in MCZ). State label only, 1 paratype no. 3027 (ANSP); 1 (UK).

Biology. The available information on the species has been presented by Hamilton (1897). He found the first specimen in December, 1872, "about a foot under ground beneath a large impacted boulder in a wild mountainous place." Several individuals were seen but only one was collected because the pale color and remarkable swiftness led Hamilton to believe they were young roaches. This and a second specimen found dead by Hamilton the following June on a wooded hillside were those which Horn had for description. Other specimens were taken later by other collectors in winter months under bark, under stones, and by sifting decaying leaves. A group of twelve was taken in late November under a log in a wooded ravine around a large dead elaterid beetle larva upon which they were probably feeding. I have not seen specimens taken since the turn of the century.

Catopocerus ulkei Brown
Fig. 4, 5; Map 1

Catopocerus ulkei Brown 1933; 215. Holotype female in CNC, seen. Type locality; District of Columbia.

Pinodytes cryptophagoides Mannerheim (in part), Horn, 1880: 249; 1892: 46; Hamilton, 1894: 16. Misidentified.

Diagnosis. The species is separated from others by its small size, the subequal second and third antennal segments, and the flattened, downward curved tip of the aedeagus.

Redescription. Length 1.4-2.2 mm. Width 0.71-0.94 mm. Color uniform dark reddish-brown, shining. Shape oblong.

Head with trace of eyes as depigmented spot on side of head in some pale specimens; vertex finely punctulate, finely striolate. Antennae well supplied with hairs throughout length; segments VII, IX, X supplied with dense vestiture of long and short hairs; I stout; II and III equally long; III narrower at base than II; IV, V, VI equal, globose; VII as long as broad; VIII smaller than VII, larger than

	Range		Mean		Standard Deviation	
	males	females	males	females	males	females
HW	0.44-0.51	0.44-0.54	0.49	0.50	0.024	0.034
PW	0.81-0.91	0.80-0.91	0.85	0.88	0.034	0.054
PL	0.54-0.63	0.54-0.64	0.59	0.60	0.30	0.047
EL	1.08-1.20	1.10-1.28	1.15	1.12	0.052	0.071
EW	0.80-0.92	0.84-0.99	0.88	0.90	0.034	0.045
PW/PL	1.41-1.58	1.41-1.54	1.48	1.46	0.05	0.05
EL/EW	1.28-1.36	1.29-1.38	1.32	1.34	0.03	0.03
PW/HW	1.72-1.86	1.70-1.86	1.77	1.77	0.05	0.04
EW/PL	1.42-1.56	1.45-1.60	1.50	1.51	0.05	0.06

Table 1. Variation in a sample of a population of Catopocerus ulkei topotypes from the District of Columbia. 10 males and 10 females. Measurements in millimeters.

VI; IX smaller than X, larger than VII; IX and X broader than long; XI conical.

Pronotum widest just behind middle; sides evenly arcuate; narrower at front than back; hind angles slightly obtuse; front angles rounded; front margin slightly concave; hind margin straight; disc finely and sparsely punctulate; finely striolate.

Elytra fused; at base slightly wider than base of pronotum; widest at middle; sides slightly curved; narrowing in apical third; surface finely punctate, some punctures vaguely indicating striae; finely striolate; apical declivity smooth.

Protibia widening to apex in distal 2/3; setose on apical half of inner margin; mesotibia gradually widening to apex in apical 2/3; inner margin setose in apical third, faintly sinuous; outer margin spinose; outer apical angle truncate. Metatibia gradually widening to apex; outer margin smooth; inner margin smooth to serate; outer apical angle slightly truncate.

Male first four protarsomeres dilated and supplied with long lateral hairs; first three mesotarsomeres feebly dilated. Aedeagus in lateral view arcuate; ventral surface of anterior end projecting forward and curved downward; tip dorsoventrally flattened and turned downward forming 80°-100° angle with ventral surface of aedeagus; parameres long and thin, exceeding tip of aedeagus, hinged at aedeagus base to ventrally deflected elongate basal pieces (figs. 4, 5).

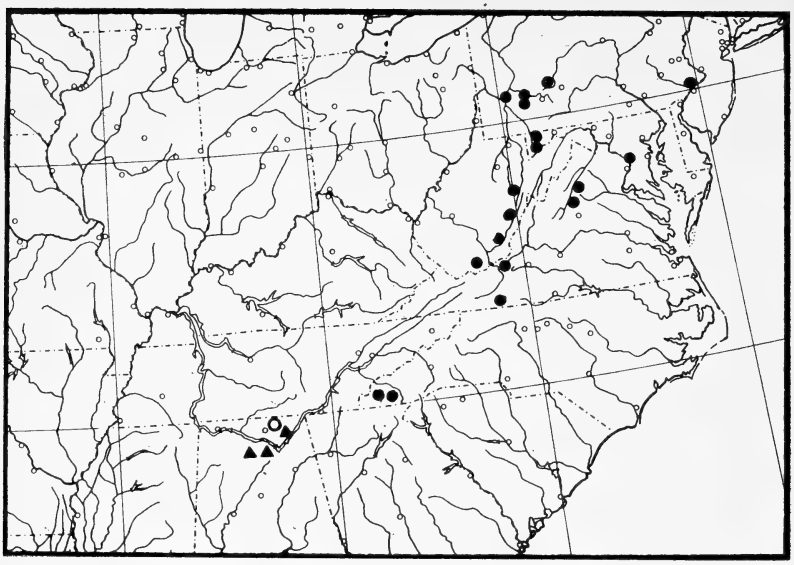
Female tarsomeres not expanded; abdominal segments as in male.

Variation. Table 1 presents meristic variation for the topotypic population. All populations examined which are assigned to this species have aedeagi of the males identical to aedeagi of the topotypic population but for two exceptions. The two samples from southwestern North Carolina are 220 air miles to the southwest of the next nearest locality from which males have been collected. These southwestern collections differ in the angle of deflection of the aedeagal tip. A distinct acute angle of about 80° is formed between the ventral surface of the aedeagus and the tip of the aedeagus. All other populations possess aedeagi in which the angle is usually slightly obtuse. Only rarely is it a right angle.

The variation of measurements for a sample of four males and eight females from Joanna Bald, Cherokee County, North Carolina, when compared to that in table 1, showed that the size of the southern populations is larger, but there is a great deal of overlap within the range of the measurements. Variation of the ratios, when compared to the topotypic population shows less difference, and that which does exist is contained within an overlap of one standard deviation from each mean. This numerical data demonstrates little or no difference from the topotypic *C. ulkei.* Since there is a large gap in knowledge of the range of the species between western Virginia and southwestern North Carolina, I am unwilling to interpret the taxonomic significance of the greater curvature of the tip of the aedeagus in the southwestern North Carolina populations. It may be a distinct subspecies if its distribution is geographically separated from typical *C. ulkei.* Or the population may represent one end or segment of a cline of gradual deflection of the aedeagal tip. Further collecting may tell.

Distribution. The species is known to occur in southwestern and southeastern Pennsylvania, the District of Columbia, Maryland, North Carolina, Virginia, and West Virginia (map 1). Future collecting might show it to be continuously distributed along the Piedmont and eastern edge of the Appalachians to the southern known locality in Cherokee County, North Carolina.

Material examined and habitat data. District of Columbia: no other data, 32. Washington, D. C., 1; 1.5, 1; 5.3, 1; Hubbard & Schwarz. Maryland: Garrett Co.; Deer Park, 4.7, 1, Hubbard & Schwarz; 2 mi. E. Keysers Ridge, 2500′ elev., 18.vi.1968, S. Peck, 3 in 220 lbs. log-stump litter. North Carolina: Cherokee-Graham County; Andrews, Joanna Bald, 4700′ elev., 26.vii.1967, S. Peck & A. Fiske, 13 in 89 lbs rotted chestnut log; Joanna Bald, 5.viii.1960,



Map 1. East central United States and *Catopocerus* distributions. Closed dots, *C. ulkei.* Open dot, *C. alabamae.* Closed triangles, *C. jonesi.*

T. C. Barr, 1 male. Clay-Macon County; Tusquitee Bald, 4.viii. 1960, T. C. Barr & M. C. Bowling, 1 male. Pennsylvania: x, 1. Allegheny County; Pittsburgh, x, 3. St. Vincent, 9. Cambria County; Nicktown, M. Wirtner, 3. Philadelphia County; 28.vi. 1911, G. M. Greene, 1. Westmoreland County; Chestnut Ridge, E. of Youngstown, 27.vi.1961, W. Suter, 1 in litter under *Rhododendron;* 11.vii.1961, W. Suter, J. Wagner, D. Reichle, 1 in forest litter. Jeannette, vii, 2; ix, 3; x, 1. Virginia. Caroll County; Groundhog Mt., 2900′ elev., Blueridge Parkway, 23.vii.1967, S. Peck & A. Fiske, 1 female in 46 lbs. rotted stump and log litter in *Rhododendron* thicket. Giles County; Mountain Lake, 1-5.vii.1970, W. B. Muchmore, 8. Madison County; Shenandoah National Park. Dark Hollow Falls, 2.iv.1967, S. Peck, 1 under rocks. Lewis Mt., 2000′ elev., 10.vi.1967, S. Peck, 104 in rotted logs. Page County; Shenandoah National Park. Hawksbill Mt., 17.x.1954, D. G. Kissinger, 1. Stony Man Overlook, 2.iv.1967, S. Peck, 3 under rocks and 6 in litter. West Virginia. Greenbrier County; outside Arbuckle Cave, 14.vii.1970, W. B. Muchmore, 1 in litter. Mercer County; 5.5 mi. N. Princeton, Brush Creek Falls, 13.v.1971, W. Shear, 1 in cliffside litter. Pocahontas County; W. side Cranberry Glades, base of mountain, streamside, under rock, 28.vi.1967, T. C.

Barr, 1 female. Hills Creek Falls, 6.v.1970, W. Shear, 1; 19.vi. 1971, Shear and Platnick, 2. Randolf County; Bickle Knob, 3800′ elev., E. of Elkins, 19.vi.1968, S. Peck, 34 in 179 lbs. of log litter. 5 mi. S. Whitmer, 18.vii.1971, S. Peck, 3000′ elev., 34 in litter. (AMNH, CAS, CM, CNC, FMNH, INHS, SBP, SVAM, UK, USNM).

Catopocerus appalachianus New Species
Fig. 6, 7; Map 2

Holotype male (MCZ no. 32228) from Balsam Gap, 5500′ elev., Mt. Mitchell, Yancey Co., North Carolina, 9.vi.1967, S. Peck. Paratypes: all material listed in section on material examined.

Diagnosis. Most similar to *C. ulkei* but differing distinctly from it and all other species in the shape of the aedeagus. Usually differing from *C. ulkei* in its larger size and greater EW/PL ratio.

Description. Length 2.14-2.86 mm. Width 0.83-1.10 mm. Color uniform dark reddish-brown, shining. Shape oblong.

Head with faint trace of eyes as depigmented spots on side of head in pale specimens; vertex finely punctulate, finely striolate. Antennae with long hairs throughout length; segments VII, IX, X with dense vestiture of long and short hairs; segment I stout; II stouter and only slightly shorter than III; IV, V, VI subglobose and subequal; VII as long as broad, widest at apical third; VIII as long as and wider than VI, smaller than VII and IX; IX and X of equal length, X wider; XI conical.

Pronotum widest at basal third; sides evenly arcuate; narrower at front than back; hind angles slightly obtuse; front angles rounded; front margin slightly concave; hind margin straight; disc finely and sparsely punctulate; finely striolate.

Elytra fused; at base slightly wider than base of pronotum; widest near middle, sides slightly curved; narrowing in apical third; surface finely punctate, punctures indicating striae; finely striolate; apical declivity smooth.

Protibia widening to apex in distal 2/3; setose on apical half of inner margin; a few spines on apical half of outer margin. Mesotibia straight along outer margin; expanding gradually along inner margin to apex from proximal third; inner margin setose in apical third, faintly sinuous; outer margin spinose; outer apical angle rounded. Metatibia gradually widening to apex; outer margin smooth; outer apical angle slightly truncate, possessing two large spines; dorsal surface of apical end with patch of setae; slight downward bow in middle in lateral view.

	Range		Mean		Standard Deviation	
	males	females	males	females	males	females
HW	0.49-0.70	0.48-0.63	0.60	0.55	0.070	0.054
PW	0.81-1.15	0.84-1.08	1.01	0.95	0.097	0.080
PL	0.58-0.80	0.55-0.75	0.70	0.68	0.072	0.064
EL	1.15-1.55	1.19-1.54	1.40	1.34	0.131	0.107
EW	0.84-1.14	0.89-1.10	1.00	0.98	0.094	0.074
PW/PL	1.36-1.55	1.43-1.60	1.44	1.49	0.05	0.04
EL/EW	1.34-1.44	1.32-1.42	1.36	1.38	0.04	0.04
PW/HW	1.58-1.82	1.69-1.80	1.66	1.74	0.06	0.04
EW/PL	1.90-2.09	1.98-2.24	1.99	2.10	0.06	0.07

Table 2. Variation in a sample of a population of Catopocerus appalachianus from Mt. Mitchell, North Carolina. 15 females and 15 males. Measurements in millimeters.

Male first four protarsomeres expanded and with long hairs; first three mesotarsomeres feebly dilated; metatibia with inner edge weakly to strongly serrated. Aedeagus in lateral view robust and arcuate; ventral surface of anterior end projecting forward; from base narrowing slightly for 2/3 length, narrowing markedly in distal third, tip slightly downcurved; in ventral view sides expanding slightly for 2/3 length, then evenly converging to tip; tip flattened; parameres gradually tapering to thin point which extends beyond aedeagus tip; basal piece of parameres pointing forwards along sides of aedeagus (figs. 6, 7).

Female tarsomeres not expanded; abdominal segments as in male; inner margin of metatibia smooth.

Variation. Table 2 presents meristic data on the topotypic population. In some specimens the outer margin of the elytra at the anterior angles bears a few coarse, low teeth. The males of the species variably possess a saw-toothed inner margin of the hind tibia, ranging from absent to highly developed.

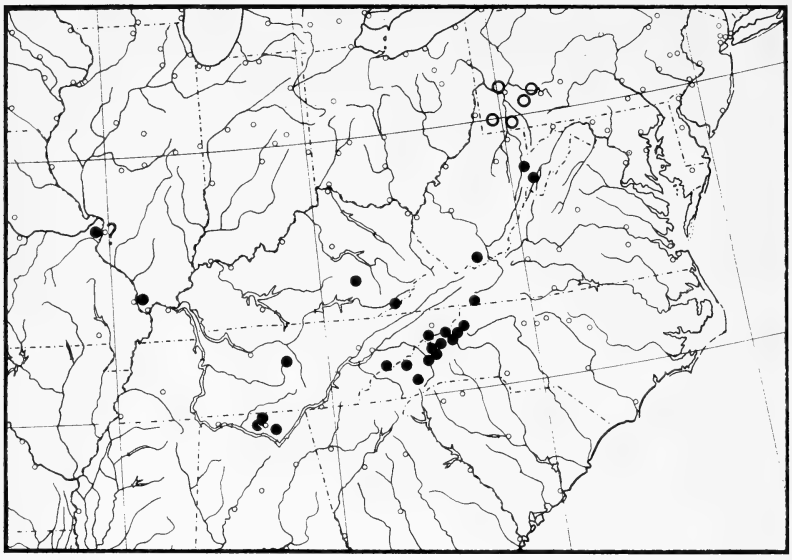
The variation in size and proportions within this species overlap in some measured populations with *C. ulkei* size and proportions. Hence, care should be used in separating the species using external criteria. A sample of four males of *C. appalachianus* from Whitetop Mt., Virginia is composed of noticeably smaller individuals. Their

PL mean corresponds to that of the topotypic population of *C. ulkei*. The Whitetop Mt. sample EW/PL mean also corresponds to that of topotypic *C. ulkei* and not the topotypic *C. appalachianus* sample. This size overlap demonstrates the clear value of using the distinct and less variable features of the aedeagus. Because of these size similarities some female specimens may be difficult to indentify. Locality records for these two species in their zone of overlap may be treated with certainty only when males are present.

Etymology. The name refers to the Appalachian region in which the beetle is found.

Distribution. The species has roughly a linear range of 480 miles along the Appalachian Mts. from Madison County, Alabama northeastward to Pocahontas County, West Virginia (Map 2). It is known from a few intermediate areas in Virginia, Tennessee, and especially from North Carolina in the vicinity of Mt. Mitchell. One collection has been made in the Cumberland Plateau of Kentucky and one in the Shawnee Hills of Southern Illinois.

Material examined and habitat data. ALABAMA. Madison County: Barclay Cave, 26.vii.1965, S. & J. Peck, 1 in trap; 18.viii.1965, S. & J. Peck, 1 in trap; 20.viii.1965, S. & J. Peck, 1 in trap; 1.ix.1965, S. & J. Peck, 2 in trap; 2.vii.1967, S. Peck and A. Fiske, 1 at carrion bait; 24.viii.1971, S. Peck, 1 at bait; 10.v.72, S. Peck, 4 at bait; 13.vii.1973, S. Peck, 1 at bait. New Hope, Cave Spring Cave, 23. viii. 1971, S. Peck, 3 at bait in side chamber 400′ in cave. Ellis Cave, 5.vii.1967, S. Peck and A. Fiske, 2 at carrion bait; ix.1968, S. Peck, 8 at carrion bait; 2 reared from eggs laid in culture 3.viii.1969, S. Peck. ILLINOIS. Union County; Pine Hills Field Station, 15.v. 1967, J. M. Campbell, 1 at malt trap site #9. KENTUCKY. Harlan County; Big Black Mt., 4000′ elev., 11.vii.1968, S. Peck, 1 in 302 lbs. log and stump litter. Jackson County; The Rises, S. Fork Station Camp Creek, 16.ii.1967, T. Marsh, W. Andrews, 1 in log berlese. NORTH CAROLINA. Avery County: Beech Mt., 15.vii.1960, Barr and Bowling, 10; Grandfather Mt., 22.viii.1960, Barr and Bowling, 1 male. Blowing Rock to Linville, 3000-4000′, 7.ix.1930, P. Darlington, 1. Buncombe County: Asheville, A. P. Jacobs, 1. Blue Ridge Parkway, 5 mi. W. Craggy Gardens, 3500′ elev., 22. vii.1967, S. Peck and A. Fiske, 6 in 63 lbs. Chestnut stump litter; Craggy Dome, 22.vii.1960, Barr and Bowling, 9. Haywood County; Richland Balsam, 1.viii.1960, Barr and Bowling, 3. Henderson County; 0.3 mi. S.W. of Bat Cave, 1000′ elev., 22.vii.1967, S. Peck and A. Fiske, 2 in 39 lbs. of log and leaf litter. Madison County; Rich Mt., 3000′ elev., 25.vii.1967, S. Peck and A. Fiske, 4 in 85 lbs.



Map 2. East central United States and *Catopocerus* distributions. Open dots, *C. hamiltoni*. Closed dots, *C. appalachianus*.

of rotted stump. Mitchell County; Blue Ridge Parkway, mile 326.8, 3200′ elev., 22.vii.1967, S. Peck and A. Fiske, 2 in 64 lbs. of litter at base of large dead pine tree: Roan Mt., 5000′ elev., 25.vii.1967, S. Peck and A. Fiske, 2 in 72 lbs. of litter along rotted beach log. Round Knob, 27.6, Hubbard and Schwarz, 1. Yancey County; Hamrick, 3000-3100′ elev., 30.xii.1946, Hairston, 1 in leaf litter: Mt. Mitchell, Balsam Gap, 5300′ elev., 9.vi.1967, S. Peck, 9 in birch-beech litter: Mt. Mitchell, 5500′ elev., 9.vi.1967, S. Peck, 10 in birch-beech litter and 1 in basal tree hole: Mt. Mitchell, 4000′-6000′ elev., June 1939, E. D. Quirsfeld, 10: Mt. Mitchell, 26 with no other data: Valley of Black Mts., July 28, 1906, W. Beutenmuller, 3; August 19, 1906, W. Beutenmuller, 1. Black Mts., vi-vii.1902, Van Dyke colln., 14. TENNESSEE. Coffee County. Beech Grove, Burke Cave, 24.v.73, S. & J. Peck, 1 male, 1 female, at carrion bait. Great Smoky Mt. National Park; Chimneys, 3000′ elev., ix.19.1944, A. Nicolay, 2 females. Newfound Gap, 5000-5200′, August 31, 1930, P. Darlington, 1 female. Clingmans Dome, 7.vii.1960, T. C. Barr. Unicoi County; Unaka Mtn., 5.vii.1953, H. & A. Howden, 1. VIRGINIA. Grayson County; Whitetop Mtn., 4000′ elev. 24.vii.1967, S. Peck and A. Fiske, 10 in 77 lbs. of log

and stump litter; Whitetop Mtn., 13.vii.1960, T. C. Barr, M. C. Bowling, 4. West Virginia. Mercer County; Athens, 6.vi.1971, W. Shear, litter, 1. Randolf County; 5 mi S. Whitmer, 18.vii. 1971, S. Peck, 3000′, 11 in litter. Pendleton County; Spruce Knob, 4000′ elev., 26.viii.1964, S. Peck & T. C. Barr, 2 under rocks and 2 in litter. (AMNH, CAS, CNC, FMNH, MCZ, SBP, USNM).

The Illinois collection, separated from the rest of the species' range, is also of special interest because of the unusual nature of the habitat. The collector, Dr. J. M. Campbell, has supplied me with more detailed data on the locality, and I quote from a letter; "Malt trap no. 9 was set in a small stand of *Pinus echinata* on a very dry site on the S. W. slope near the top of a ridge. There was very little litter on the soil; what little litter there was consisted of pine needles. This entire area of S. Illinois is characterized by having very small stands of pine scattered on the S. W. slopes of dry, rocky ridges. It is possible that any beetles found in this site live in the more mesic ravines which are nearby."

This species may also exist in Missouri. One female labeled "St. Louis, Mo., iv.28" from the Liebeck collection is in the Fall collection in the MCZ. The measurements of the specimen fall into the range of variation of *C. ulkei,* but the Illinois record of *C. appalachianus* suggests that it might more likely occur in Missouri if we accept the accuracy of the specimen label

Life Cycle Data. Eight adult *C. appalachianus,* captured September 1, 1968 in Ellis Cave, Madison Co., Alabama, were kept alive in laboratory culture at 15°C in plastic dishes of moist soil from Ellis Cave. All adults had died by May 1969. Two beetles becoming adults in May 1969 died in June and July 1970, suggesting that full adult life may be about one year. Copulation occurred in culture. A total of 37 eggs were laid on the soil surface, with soil crumbs stuck to their sides. The number of females producing these eggs is not known. The month of egg laying and number of eggs were as follows: October, 10; November, 5; December, 3; January, 2; March, 14; April, 3. Reproduction may thus occur throughout the year, especially under favorable temperature conditions such as in caves or deep rock crevices. The eggs were white and oblong, a sample of six measured .35-.60 mm (mean .48 mm) by .55-.75 mm (mean .63 mm).

A sample of 8 eggs hatched 13 to 20 days (mean 17 days) after being laid. A sample of 7 larvae had a total life span in this stage of from 26 to 30 days (mean 29 days). The first instar lasted 8 days for 1 larva. The total number of instars was not determined

but may be three. Approximately the first 20 days of larval life were spent feeding on the soil surface or in shallow burrows at the edge of the yeast. Approximately the last ten days (6 to 11 recorded) of larval life were spent in deepened vertical burrows which were made into pupation chambers. The larvae in these cells became more plump and swollen. Pupation lasted from 16 to 22 days (mean of 20 in a sample of 7). After ecdysis the adults remained in their cells for about a week before emerging. When the adults became reproductively active is not known.

Some of the larvae and pupae were preserved for a study of immature characteristics. They are in the MCZ beetle larva collections and will be described in a later paper.

Catopocerus jonesi New Species
Figs. 8, 9; Map 1

Holotype male (MCZ no. 32229) from Eudy Cave, 1 mi. S. Oleander, Marshall County, Alabama, 23.vi.1942, W. B. Jones leg. Paratypes, in SBP collection: Alabama. Morgan County, Shine Cave (in Newsome Sinks) 7.vii.1957, L. Varnedoe, 1 female; Vandever Cave, 3 mi. S.S.W. Laceys Spring, 22.v.1972, S. & J. Peck, 1 male and 1 female in rotten sticks at back of cave. Jackson County; House of Happiness Cave, 4 mi. S.W. Scottsboro, 23.v. 1972, S. & J. Peck, 2 males and 1 female at carrion bait near entrance.

Diagnosis. The species can be distinguished by the third antennal segment being longer than the second, and the fifth being longer than the fourth and sixth, and by the conspicuous toothed ventral projection of the aedeagus.

Description. Holotype measurements, HW, 0.62. PW, 1.12. PL, 0.80, EL, 1.56. EW, 1.17.

Length 2.54-2.65 mm. Width 1.15-1.23 mm. Color uniform dark reddish-brown, shining. Shape oblong, sides parallel.

Head with no indications of eyes; clypeus slightly truncate; frons punctate; vertex punctate and finely striolate. Antennae well supplied with long hairs; segments IX, X, XI, possessing dense mat of long and short hairs; segment I robust; II cylindrical, shorter than III by 1/4; III conical, as broad as II; IV, VI longer than broad, shorter than V; VII distinctly longer than broad, slightly wider than VIII and longer than VIII by a third; IX slightly narrower than X, a third wider than VIII; XI conical at tip.

Pronotum widest at middle; sides evenly arcuate; narrower at front than back; hind angles slightly obtuse; front angles rounded;

front margin slightly concave; hind margin slightly concave; disc finely punctulate; finely striolate.

Elytra fused; at base slightly wider than base of pronotum; widest near middle; anterior margins subparallel; surface punctate, punctures indicating striae; finely striolate; sides and apex smooth. Protibia straight on outer margin; sinuous on inner margin; widening to apex in apical 2/3; setose on apical half of inner margin; spinose along outer margin; two large spines at outer apical angle; two shorter spines on inner margin at origin of tarsus; comb of short spines below origin of tarsus. Mesotibia straight and spinose along outer margin; curved and setose along inner margin; expanding to apex in apical 2/3; outer apical angle sharp, possessing two spines; one large spine along ventral edge of apical margin. Metatibia stout, gradually widening to apex; outer and inner margin smooth; curved slightly so that apex is deflected outward; straight in lateral view; one large spine at outer apical angle and one in middle of apical margin; dense patch of setae along upper and inner margin of apex. Fifth abdominal segment evenly rounded.

Male first three protarsomeres widely expanded and supplied with a dense mat of hairs; first three mesotarsomeres less expanded and hairy. Aedeagus in lateral view bent near base, basal anterior projection deflected downward, body of aedeagus slightly sinuous and tapering, ventral surface projecting posteriorly to form shelf under genital orifice, dorsal surface curving downward slightly; in ventral view robust, sides parallel, dorsal surface tapering only at apex and smooth in outline, ventral surface with apical tooth-like projection; parameres gradually tapering to point, terminating close to aedeagal apex, basal pieces thin (figs. 8, 9).

Female tarsomeres not expanded.

Variation. No noteworthy variation is evident in the seven known specimens.

Etymology. I am pleased to name this species for Dr. Walter B. Jones, retired State Geologist of Alabama, in recognition of his assistance to me and to other students of Alabama cave fauna.

Distribution. Known only from Morgan, Marshall and Jackson Counties in northeastern Alabama (map 1).

Catopocerus alabamae New Species

Figs. 10, 11; Map 1

Known only from Holotype male (MCZ no. 32230) from Cave Spring Cave, Chapman Mtn., 1 mi. N.E. Huntsville, Madison Co.,

Alabama, found in the stomach of a plethodontid salamander *Eurycea lucifuga,* captured 8.ix.1965, S. Peck leg.

Diagnosis. Most similar to *C. jonesi* but differing from it and all other species in the shape of the aedeagus, the very widely expanded male tarsal segments, and the distinct setal bearing excavation on the inner and upper margin of the hind tibia.

Description. Measurements of the Holotype. HW, .70. PW, 1.25. EL, 1.78. EW, 1.30. Color uniform dark reddish brown, shining. Shape rectangular, rounded at front and back.

Head with no traces of eyes; vertex finely punctulate; frons coarsely punctate. Antennae with hairs on all segments; segments IX, X, XI also supplied with dense cover of short hairs at their apical margins; segment I stout; II shorter than III, III slightly conical; IV, VI larger than broad, shorter than V; VII larger than wide, larger than VIII, smaller than IX; IX longer than wide; X as long as wide; XI conical at tip.

Pronotum widest at middle; sides evenly arcuate; narrower at front than back; hind angles slightly obtuse; front angles rounded; front margin slightly concave; hind margin slightly concave; disc finely puntulate, coarsely set with punctures.

Elytra fused; at base slightly wider than base of pronotum; widest near middle; surface finely punctulate, with larger punctures indicating 5 distinct and a sixth indistinct stria. Protibia widened at apex, protarsi conspicuously expanded and setose. Mesotibia widened at apex, mesotarsi conspicuously expanded and setose. Metatibia with setae bearing excavation in posterior third of dorsal and inner surface. Metatarsi not expanded. Fifth abdominal segment evenly rounded.

Aedeagus in lateral view (fig. 10) wide, without ventral projection, expanded in posterior half. In ventral view (fig. 11) wide and slightly expanded toward posterior. Parameres gradually tapering, terminating close to aedeagal apex, basal pieces thin.

Notes on holotype. The tip and left side of the aedeagus were damaged in dissection. The illustrations are reconstructed except for the dorsal tip whose full size and shape are not known.

Etymology. The name refers to the state of Alabama.

Distribution and habitat notes. The species is probably a deep soil inhabitant, limited to northeastern Alabama. The type locality is a small cave under the sandstone cap of Chapman Mountain. A seep spring in the cave gives the cave its name. I have visited the cave many times since 1965 in unsuccessful attempts at obtaining more specimens by searching by hand under rocks and litter and by

using bait. The salamander which obtained the beetle as food undoubtedly did so from a small and/or inaccessible population in or near the cave. *Catopocerus* are not commonly eaten by terrestrial cave salamanders. I have examined the digestive tract contents of 433 salamanders from caves within the range of *Catopocerus* in the southeastern U. S. (Peck, 1974: Richardson and Peck, in MS) and no other *Catopocerus* have been found.

Evolution and Distribution

We may assume that the genus had a past transcontinental range. The present division of the generic range into the ecologically isolated eastern and western forested regions may date from the Miocene when drying conditions caused a retreat of the Neotropical flora from western North America. This range division was probably widened with the later Pliocene arid trend associated with the northward invasion of the Madro-Tertiary geoflora which gave rise to the recent xerophytic vegetation (Axelrod, 1958).

Since this division, there is little that can be said of speciation and distributional events for the eastern species. A more rich history is evident in the western species, but will be discussed in a later paper. The three eastern species with limited distributions (*C. hamiltoni, C. alabamae,* and *C. jonesi*) probably experienced a contraction to their present ranges, from a wider ancient range, in connection with Pleistocene climatic events. None of these species is closely related to the other.

C. applachianus and *C. ulkei,* however are similar enough to have been derived from a single common ancestral species which may have inhabited the Appalachians from at least Pennsylvania to North Carolina. A division of the range into two main units during an early interglacial may have allowed *C. ulkei* to diverge in the north from Virginia perhaps to Pennsylvania, and allowed *C. appalachianus* to diverge in the south in North Carolina. *C. ulkei* may have then dispersed southward during the Illinoisan glaciation to southwestern North Carolina. These populations may have become isolated and somewhat divergent during the Sangamon interglacial. Other overlap of the ranges of the two species may have occurred by dispersal in the Illinoisan, as well as the Wisconsinan. However, judging from the lack of other geographic variation, most of the present distributions were probably gained in the Wisconsinan. This was the time when the larger and perhaps more vagile *C. appalachianus* moved north into Virginia and West Virginia. The populations of this species in

the Cumberland Plateau of Kentucky and Alabama, the Highland Rim of Tennessee, and the Shawnee Hills of southern Illinois are probably not remnants of an ancient distribution but also date from the Wisconsinan glaciation when more wet and cool montane-type climatic conditions prevailed in the Interior Basins, favoring the distribution and dispersal of "montane" beetles.

The comparatively large ranges and low levels of geographic variability in *C. ulkei* and *C. appalachianus* are remarkable in the light of an assumed low dispersal potential resulting from the beetles' winglessness, eyelessness, and soil habitation. Other ecologically similar beetles, for instance *Anillinus* and *Arianops* (Barr, 1969; 1974) in the eastern United States have much smaller ranges and are more highly speciated. In contrast then, it must be that the vagility of some *Catopocerus* is higher than would seem likely at first, because of an incompletely understood ability to withstand various mechanisms of long distance dispersal, similar to that of some European soil Colydiid beetles (Peck, 1972).

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POST-IMMOBILIZATION WRAPPING OF PREY BY LYCOSID SPIDERS OF THE HERBACEOUS STRATUM[1]

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The use of silk for wrapping prey is generally associated with those spiders that construct trapping webs; nevertheless, there are indications in the literature that wandering spiders sometimes use silk for this purpose. In some of the latter cases the silk is applied after the prey has been subdued by biting, a use corresponding to that of the diguetid and linyphiid web-weavers studied by Eberhard (1967). Post-immobilization wrapping in the latter two families was suggested to prevent the prey from falling out of the web during subsequent attacks (ibid.), and in araneid spiders to have the same and additional roles, depending on species and prey size (Robinson et al., 1969). The function of this behavior in the non-web-weaving ctenids (Melchers, 1963), theraphosids (Eberhard, 1967), and lycosids (Rovner, 1971) remained unknown and was the subject of the present study. Our findings suggested that post-immobilization wrapping by wandering spiders serves the same general function that it probably does in web-weavers — to prevent prey from dropping from the spider's elevated location down to the ground whenever it is released from the chelicerae during feeding, grooming, or subsequent capture attempts.

Methods

We observed individuals of *Lycosa rabida* Walckenaer (females = 12-19 mm), *Lycosa punctulata* Hentz (females = 13-15 mm), and *Schizocosa crassipes* (Walckenaer) (females = 8-10 mm) for the presence of and nature of prey wrapping. Whereas *S. crassipes* was collected during spring on forest leaf litter, both species of *Lycosa* were found in grassy fields, *L. rabida* during the summer and *L. punctulata* during early fall. The spiders were collected in Athens Co., Ohio, USA.

Spiders were housed individually in plastic cages (70 × 125 × 70 mm high) with water available ad lib., and given mealworms (larvae of *Tenebrio molitor*) for maintenance feedings. Laboratory

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temperatures averaged 25.8 ± 2.7° (SD) over the entire investigation.

Initial observations were made on spiders in boxes identical to their housing cages. Each individual had been food-deprived for up to 7 days. In this phase of our study we used the following types of prey: terrestrial isopods (*Armadillidium* sp.), 6-8 mm; Japanese beetles (*Popillia japonica*), 10-12 mm; mealworm larvae, 18-20 mm; small grasshoppers (Cyrtacanthacridinae), 6-8 mm; small ground crickets (Nemobiinae), 10-13 mm; and vestigial-winged fruit flies (*Drosophila melanogaster*), 2 mm. We offered three prey at time = 0, and additional single prey at +10 and +20 min (all of the same species) in most of these tests. (For fruit flies, groups of eight were added at each of the three times.) Observation periods were at least 30 min in duration. The spider then was returned to its home cage with its captured prey.

To determine the functions of the various spinnerets in wrapping, we sealed pairs of spinnerets with paraffin while female *L. rabida* were under CO_2 anesthesia. Two females underwent sealing of the anterior spinnerets; two had the anterior and median spinnerets sealed; and two, the median and posterior spinnerets. These spiders were subsequently observed and filmed (Bolex Macrozoom Super 8 mm camera, Model 160) during prey-wrapping. We also examined the silk on the prey and substratum, after chasing away the female from her just-wrapped prey.

To study the preference of *L. rabida* (and, to some extent, *L. punctulata*) for the ground vs. the herbaceous stratum, we constructed artificial "field habitats" in three terraria (0.2 × 0.4 × 0.2 m high). Cardboard "foliage" was fixed in a plaster base which provided the "ground surface" on ¾ of the terrarium bottom. The remainder of the glass bottom was left uncovered to provide an alternative ground surface in case the plaster had a repellent effect on the spiders (which turned out not to be the case). Vertical and sloping surfaces projecting into space were provided by the artificial foliage (Fig. 1). Spiders could climb to a height (limited by a glass lid) of 0.19 m.

Three female *L. rabida* (tagged with non-toxic enamel) were housed in each terrarium. (Three individuals were cannibalized in the course of this experiment and were replaced with equivalently tagged substitutes.) To prevent possible conditioning effects, we fed the spiders on the ground as often as on the foliage. (Feeding was done at times other than the daily observation periods.) We observed the nine spiders for 2-hr blocks of time each day for 10 days during

Fig. 1. Female *Lycosa rabida* (with prey) on artificial foliage.

the afternoon (on most days, 1300-1500), and recorded the duration of time each spider spent on the ground vs. the foliage. At ½-hr intervals we also measured the height of those spiders that were on the foliage. After completing this phase of our study, we observed and filmed prey capture and wrapping by spiders on the artificial foliage. Analysis of these and other films was aided by use of a Bell & Howell Super 8 mm Multi-motion projector.

Field observations were made on *L. rabida* during daylight hours (usually 1300-1500), and during both day (1300-1500) and night (2030-2200) conditions on *L. punctulata.* The spiders were detected at a distance and their location within the habitat noted. By approaching carefully, we were able to film undisturbed *L. rabida* in the field.

Prey-wrapping Behavior

Whereas individuals of *S. crassipes* did not use silk after prey capture, those of *L. rabida* and, to a lesser extent, *L. punctulata* did so. In the latter two species, silk was not used to immobilize the prey, since wrapping began after the prey had ceased most of its struggling, usually several min after capture (Table 1).

Table I. Bouts of prey-wrapping by female *Lycosa rabida* (*) and *Lycosa punctulata* (†) when offered multiple prey during a 30-min period. A total of 12 spiders was tested on each type of prey. (Sample sizes in parentheses.)

Prey	Bouts/ captures	Mean revolutions/ bout	Mean duration (sec)	Mean onset after bite (min)
*Mealworms	16/40	4.5(15)	36(13)	11.4(8)
*Grasshoppers	28/27	4.4(27)	34(22)	2.7(9)
*Crickets	50/40	3.2(48)	26(39)	1.1(8)
†Crickets	6/32	2.2(6)	16(6)	9.3(3)

When beginning a bout of wrapping, the spider spread and wiggled its spinnerets, flexed its abdomen ventrad, and then pressed its anterior spinnerets to the substratum. (Sometimes additional attachment disks were placed on the substratum in this manner within an arc of 60° or less.) Then the spider began to pivot above the prey. In about 10% of the cases the spider pivoted ¼ revolution (or sometimes ½ revolution), fixed an attachment disk to the substratum, and then began to turn in the opposite direction. However, in most cases the spider pivoted in only one direction, while remaining centered above the prey. During the first revolution, the silk was attached to the substratum at 2-5 points, the number perhaps depending on the prey's bulk. Fewer attachment disks were placed during the next turn or two, and usually only one or none during later revolutions.

During the first two or three turns, the spider usually held the prey in its chelicerae (Fig. 2). Consequently, as the spider revolved, the prey animals beneath it pivoted around with the spider. (Very large animals, while not held in the chelicerae during wrapping, and therefore not having their weight supported by the spider, were contacted by the palps, chelicerae, and sternum of the spider pivoting above.) If, as was the case with most prey, the spider held the prey in its chelicerae during early revolutions, it then released the prey during a subsequent turn and continued to pivot for one or more revolutions (Fig. 3). Throughout the process, the palps were used to contact or manipulate the prey. In *L. rabida* 80% of the wrapping bouts involved four or fewer revolutions (mean = 3.3 ± 2.1 SD; range = 1-14; n = 106). Some views of one such bout are sketched in Fig. 4.

All three pairs of spinnerets were used during prey-wrapping. Data obtained from experimental animals indicated the same roles

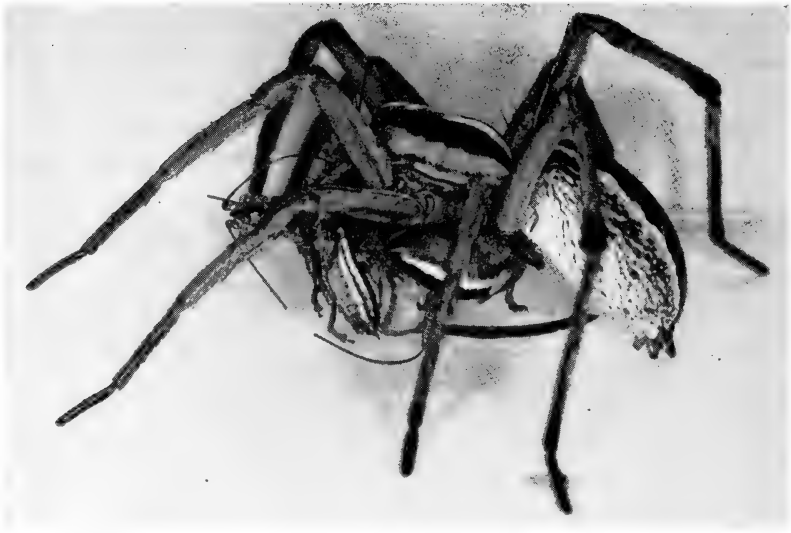


Fig. 2. Female *Lycosa rabida* placing an attachment disk on the substratum during the early phase of prey-wrapping. The multiple prey are held in her chelicerae and palps.

Fig. 3. Female *Lycosa rabida* during the later phase of prey-wrapping. The prey have just been released from her cheliceral grasp. (Her palps continue to contact the prey.) Swathing silk issues from her posterior spinnerets.

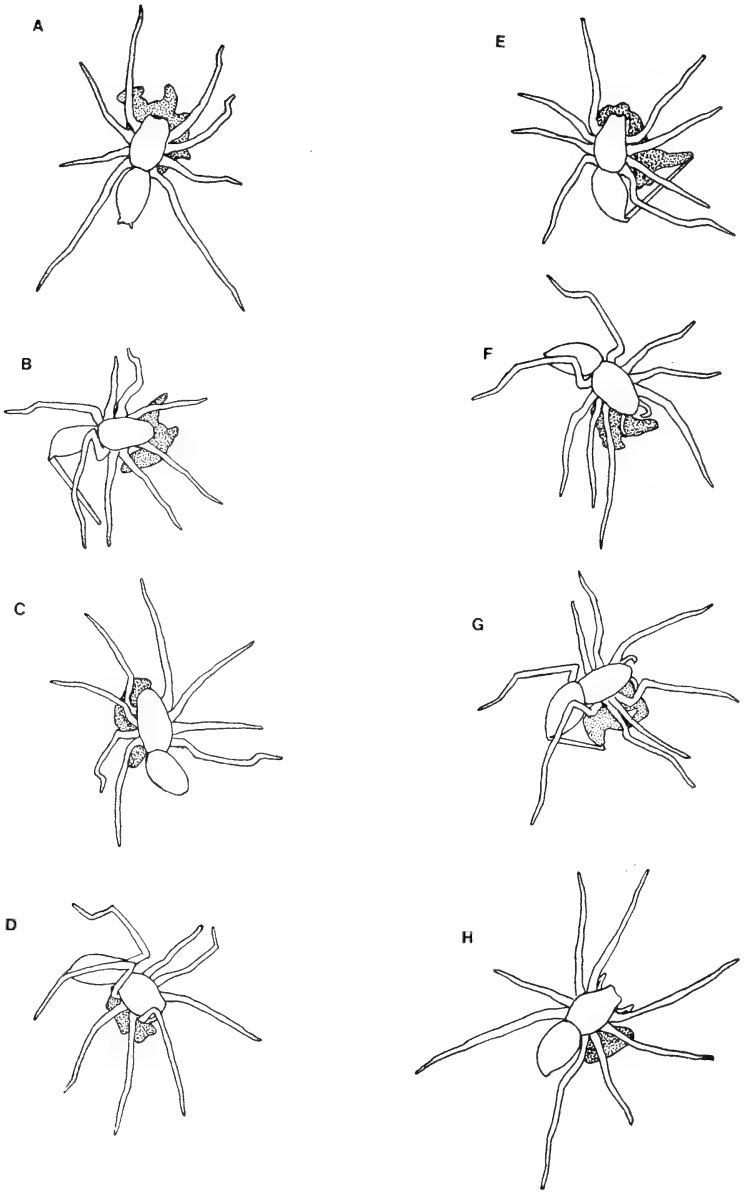
for the spinnerets in lycosids as in other spiders that wrap prey. When the anterior spinnerets were sealed, no attachment disks were produced. The prey was wrapped but not fixed to the substratum. The same was true when the anterior and median spinnerets were sealed. When the median and posterior spinnerets were sealed, attachment disks were fixed to the substratum and dragline laid around the prey, but no swathing silk. In this case wrapping was not effective. Multiple prey were not tied together; indeed, the prey items were often pushed apart by the legs of the pivoting spider.

As the result of normal wrapping behavior, silk was placed around the bodies of the prey animals and attached to the substratum at intervals. Although the pivoting spider had pulled the threads taut, the silk was not dense enough to produce a very tightly wrapped package, as is produced by orb-weavers, for example. Indeed the wrapping was so sparse that it would be unnoticed by the casual observer. Nevertheless, the prey group did form a more compact mass than it had prior to wrapping. When the spider resumed feeding, it lifted the prey away from the substratum a short distance (rather than lean down to feed); however, the lines running to the substratum generally remained intact due to their elasticity.

After prey-wrapping, the spider sometimes groomed its chelicerae and palps, while remaining directly above the prey, and then resumed feeding. Additional prey that approached within reach were often captured; and one or more bouts of wrapping followed. However, regardless of whether further captures were made after the first bout of wrapping, subsequent bouts on the previously wrapped prey occurred later in the observation period in many cases.

Table II. Number of *Lycosa rabida* making single vs. multiple captures when offered multiple prey during a 30-min period (second figure) and the number of those captures in which wrapping occurred (first figure). Twelve spiders of each sex were tested on each type of prey.

Prey	Males		Females	
	Single capture	Multiple capture	Single capture	Multiple capture
Isopods	—/ 0	—/0	1/ 4	—/ 0
Beetles	0/ 1	—/0	2/ 6	—/ 0
Mealworms	0/ 9	—/0	1/ 3	8/ 9
Grasshoppers	2/ 7	2/2	1/ 1	11/11
Crickets	0/ 4	2/3	—/ 0	12/12
Totals	2/21	4/5	5/14	31/32


A
B
C
D
E
F
G
H

L. rabida wrapped various types of prey, especially in situations in which multiple prey were captured (Table II). While only 19% of the males captured multiple prey, 68% of the females did so. Considering both sexes together, wrapping occurred in 20% of the cases in which only single captures were made, and in 95% of the cases in which two or more prey were captured. Such correlations meant that females wrapped prey much more often than males, performing at least one bout of wrapping in 78% of the observation periods in which they captured prey (single or multiple), while males did so only 23% of the time. None of our spider species wrapped fruit flies.

As shown in Table I, individuals of *L. punctulata* wrapped prey much less often than *L. rabida* and did so less intensively (fewer turns and shorter bout duration). Furthermore, it was only four of the twelve females that did so; none of the twelve males wrapped prey.

Stratum Selection

Field observations. — We watched penultimate and adult *L. rabida* on sunny, calm days (early July) in a grassy field near the edge of a woods. Undisturbed individuals rested motionless on the leaves and stems of grasses and other vegetation. The spiders typically were on horizontal or sloping surfaces (rather than vertical ones). Those individuals we happened to observe were on the upper leaves of relatively low vegetation or part-way up the stems and leaves of taller vegetation.

In response to mild disturbance, the spiders walked or climbed a short distance and then resumed their motionless stance. Strong disturbance (as that which resulted from our walking near them during our collecting efforts) caused the spiders to run and climb

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Fig. 4. [Opposite page]. Sketches, based on a Super 8 mm film, showing dorsal views of prey-wrapping by a female *Lycosa rabida*. The several items of the multiple prey-capture are drawn as an homogenous mass (stippled) for convenience, and should not be regarded as a wrapped bundle. Lighting conditions permitted seeing the silk in views B, E, and G. Times were rounded to the nearest sec. A. Placing 1st attachment disk (Time=0). B. One-quarter into the 1st revolution (+ 4 sec). C. Near end of 1st revolution (+ 7 sec). D. One-third into 2nd revolution (+ 9 sec). E. Near end of 2nd revolution (+ 12 sec). Prey were released from the chelicerae at the beginning of the next revolution. F. One-third into 3rd revolution (+ 14 sec). G. Beginning of 4th revolution (+ 18 sec). H. End of 4th and final revolution (+ 21 sec).

swiftly through the foliage, sometimes breaking into a series of leaps and dashes that carried them long distances along the top of low-growing vegetation in a few seconds. Thus, these animals usually remained in the herbaceous stratum; only occasionally did an individual plunge downward and hide near the ground.

Penultimate *L. punctulata* were seen in the fall in the same fields, and typically traveled through the herbaceous stratum when disturbed. At night these spiders were seen resting on or moving slowly upon the vegetation or, much less frequently, upon the ground.

Laboratory studies. — The results of our study of diurnal stratum selection by undisturbed female *L. rabida* in an artificial habitat are summarized in Fig. 5. (Temperature was 25-26° and relative humidity > 60% throughout the 10 days.) During the 20-hr survey, the spiders were on the cardboard foliage 73% of the time. Most of that time the animals rested motionless on one of the "leaves" at an average height of 0.12 m, i.e., more than half-way up the "plant." The long axis of their bodies was usually in a plane ranging from nearly horizontal to a slope of about 60° from the horizontal. In the latter situation the spider faced up- or downward. In those cases in which the spider rested vertically on a "stem" the spider

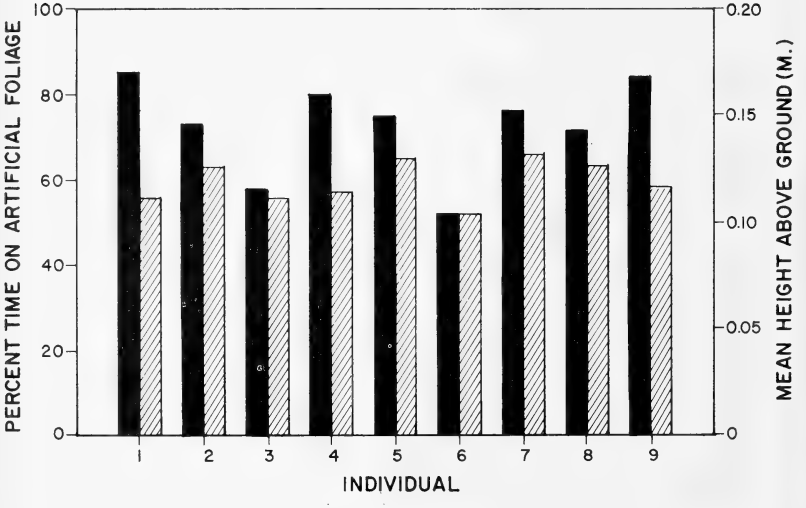

Fig. 5. Stratum selection by female *Lycosa rabida* in an artificial habitat. During 20 hr, spread over 10 days, we recorded the proportion of time spent on cardboard foliage (solid bar) vs. on the ground. At half-hr intervals within observation periods, we also measured the height of those spiders that were on the foliage (hatched bar).

typically faced downward. Individuals rested more often in an upright position on the upper surface of the leaf (illumination = approx. 400 lux) than they did in an inverted position beneath the leaf (illumination = approx. 130 lux).

We considered each spider's behavior within the 2-hr periods of observation and noted that each remained within the "herbaceous stratum" during the entire 2 hr in 5.3 (range = 4-7) of the ten periods. Each spider remained on the ground throughout the 2-hr period in only 1.6 (range = 0-3) of the ten periods. The spider moved from the ground to the foliage or vice versa in the remaining 3.1 (range = 2-4) of the ten periods.

Some observations made on several female *L. punctulata* in the artificial habitat indicated that these spiders also tended to spend their time resting on the foliage. However, we did not quantify this part of our study.

After completing the 10-day survey of stratum selection by *L. rabida,* we observed and filmed prey-wrapping by these spiders on the artificial foliage. The behavior resembled that performed on the floors of the housing containers, as we described above. Wrapping

Fig. 6. Female *Lycosa rabida* wrapping prey on artificial foliage. This leaf sloped at an angle of about 60° to the horizontal.

usually was performed at the capture site and therefore was carried out in all planes, including the vertical. The spiders behaved on sloping leaves and vertical stems in a manner similar to that seen on the horizontal cage floors; however, pivoting was slower on the narrow surfaces, apparently due to the spider's having to seek footholds as it revolved "above" the prey (Fig. 6).

In some cases, we intentionally disturbed the spider before or after prey-wrapping. In the former situation, the prey sometimes was released from the chelicerae and dropped to a lower leaf or to the ground. On the other hand, if wrapping already had occurred, they prey did not fall from the capture site when released from the chelicerae, even on a vertical surface. When multiple prey were wrapped on a sloping surface, they: (1) remained together rather than roll apart and (2) hung at the wrapping site rather than drop to the ground, when the spider was chased away.

A further bit of evidence for the adaptedness of *L. rabida* to the herbaceous stratum was provided later by the construction of a "shelter web" (about 50 mm^3) and, within it, an egg sac (infertile) by a female on a nearly horizontal leaf 0.13 m above the ground in the artificial habitat.

Discussion

Preference for herbaceous stratum. — *S. crassipes* is well-known as an inhabitant of woodland leaf-litter (Kaston, 1948; Fitch, 1963); indeed, lycosids are generally regarded as ground-dwellers (Lowrie, 1968). However, *L. rabida* and *L. punctulata* can be collected by sweeping grass and shrubs (Kaston, 1948). Kuenzler (1958) also found *L. rabida* on the lower trunk and branches of trees in open woodland. Whitcomb et al. (1963) describe finding *L. rabida* in cotton fields on the ground during the day, but at night ". . . halfway up the cotton stalks feeding on bollworm or cabbage looper moths . . ." as well as on noctuid moths. At night, Eason and Whitcomb (1965) collected 80% of their specimens of *L. rabida* 2/3 m or more above the ground in tall grass and bushes.

According to Eason and Whitcomb (1965), *"L. punctulata* is mostly captured on or near the ground, since it has less tendency to climb into bushes than does *L. rabida."* While finding both species in grassland, Fitch (1963) reported that *L. punctulata* preferred ". . . relatively open or barren situations as compared to *L. rabida,* which prefers a tall-grass habitat." Kaston (1948) stated simply that both species have the same habits.

Our field and laboratory observations are in agreement with the general idea expressed above — *L. rabida* and *L. punctulata* are adapted for spending a significant part of their life in the herbaceous stratum, rather than being, like most lycosids, ground-dwellers. (Obviously, stratum selection may vary during the life of an individual under different conditions, both external (temperature, humidity, wind, etc.) and internal (hunger, sexual state, etc.)). A difference between the species in regard to habitat or stratum selection, suggested by some authors, was not examined by us, but might be revealed by quantitative field and laboratory studies. The relatively longer legs of *L. rabida* suggests a greater adaptation to the herbaceous stratum than that of *L. punctulata,* as does the stronger tendency of *L. rabida* to wrap prey.

While these lycosids are often seen running about, perhaps migrating from one habitat to another in response to micro-climatic conditions, or perhaps merely reacting to the collector's movements, most of their time is probably spent at rest on the foliage. This seemed to be the case in the field, and was certainly the situation in the artificial habitat. As has been noted elsewhere (Edgar, 1969), lycosid spiders generally remain motionless and wait for their prey to come within reach. Like the web-weaving spiders, the wandering spiders of the herbaceous stratum are resting on a medium that provides effective transmission of vibrational cues from the prey.

Function of prey-wrapping. — We hypothesize that post-immobilization prey-wrapping in *L. rabida* and *L. punctulata* is a behavioral adaptation for life in the herbaceous stratum. It reduces the possibility of losing the prey items when the spider releases them from its cheliceral grasp between bouts of feeding. The spider may release its grasp to make an additional capture, to groom, to drink, or to locate another point on the prey's body for further feeding. Also, when startled by another animal or by shaking of the substratum due to wind, the spider's momentary release of the prey would often result in its loss. No such problem exists for ground-dwelling forms.

Our hypothesis is supported by the absence of wrapping after the capture of small prey, which are easily held in the chelicerae and ingested in a relatively short time. It appears, then, that post-immobilization wrapping serves the same primary function in wandering spiders as it does in web-weavers — to prevent the prey from dropping to the ground from the spider's elevated location. Also, it is important when multiple prey are captured by a wandering spider,

since the number of prey that the spider can hold in its chelicerae during feeding is limited.

As to the functions of the components of prey-wrapping, we suggest the following. The swathing silk serves to enclose the prey, a role that is not only important for holding multiple prey together, but which is also of value in holding together the pieces that often result from the process of ingesting a single prey item. This latter function may be one reason for the occurrence of additional bouts of wrapping during the course of feeding. The dragline may be entangled in the swathing band and serve to attach the prey package to the substratum via the attachment disks, although it seemed that the swathing band itself was connected to the attachment disks. Since attachment to the substratum seems to be of prime value in preventing loss of acquired food material, the re-anchoring that occurs in additional wrapping bouts during the course of feeding probably makes up for the breakage of lines that accompanies the physical and chemical processing of the prey by the feeding spider, and thus may be another reason for extra bouts of wrapping.

The temporal pattern is one of providing multiple attachment points, along with swathing, during the early phase of each bout (while the prey is held in the chelicerae) and then devoting most of the remaining time to swathing (after the prey has been released from the chelicerae). The early phase (attachment) may be important for effective wrapping, since it enables the spider to release the prey and pivot around it, pulling the swathing lines taut.

Role of aciniform and other silk glands. — Comstock (1912) and others have described the aciniform glands of web-weaving spiders as the source of the swathing silk used for prey-wrapping, as well as the fine fibers of egg sacs. These glands are present in lycosids, but their function had remained unknown (Richter and Van der Kraan, 1970). On the basis of histological data, Richter (1970*a*) suggested roles for the aciniform glands in lycosid spiders — in producing silk involved in molting, egg sac construction, and sperm web construction.

Our data indicate that the aciniform glands also have one of the same functions in lycosids as they do in the web-weavers — production of swathing silk for wrapping prey. When the spigots for these glands were closed experimentally (by sealing the median and posterior spinnerets), wrapping behavior was ineffective. Such spiders pivoted, fixed attachment disks, and laid a dragline; however, no broad bands of silk were placed on the prey. Indeed, the several items of multiple prey were often pushed apart by the legs of the pivoting spider.

Our sealing of the anterior spinnerets (site of spigots for the piriform glands) prevented attachment disk production, as was well-known in the literature. Such spiders could wrap the prey but not attach it to the substratum. This was also the case with spiders that had their anterior and median spinnerets sealed, with the further limitation of being incapable of producing draglines. In summary, for complete wrapping of the prey, these lycosids are using all three pairs of spinnerets and employing silk from three types of silk glands (the third being the ampullaceal glands — for production of draglines — whose spigots are on the anterior and median spinnerets). This agrees with observations made by Melchers (1961) on prey-wrapping by normal individuals of *Cupiennius salei,* a large ctenid spider.

Since the wrapping of prey by lycosids (and at least some other wandering spiders) probably correlates with a preference for the herbaceous (or higher) stratum, we hypothesize that the size of the aciniform glands, source of swathing silk, would also. This expectation is based on Richter's (1970*b*) demonstration of such a correlation between ampullaceal gland size (dragline silk) and preferred vegetation structure in *Pardosa* spp. Indeed, we should expect lycosids with larger ampullaceal glands to have larger aciniform glands, based on our hypothesis and on Richter's findings.

Stimuli releasing prey-wrapping. — The correlation between the frequencies of prey-wrapping and multiple prey-capture suggests that the latter event provides a stimulus situation to release prey-wrapping. The value of wrapping for retaining multiple prey has been discussed above. However, wrapping certainly occurs after single prey are captured, if these prey are about as large or larger than the spider's body size. It seems, then, that the stimulus for post-immobilization wrapping is that of a relatively large volume or mass of prey material beneath the spider, not the absolute number of prey captured. We suspect volume rather than weight to be the stimulus, since very large prey are wrapped without being held in the chelicerae following a capture in which the bite was maintained without the spider supporting the weight of the prey resting on the substratum.

Prey-wrapping was initiated after the prey had ceased most or all of its struggling. Groups of small crickets or grasshoppers, each member of which succumbed quickly to the spider's bite, were wrapped within a minute or two after capture. Mealworms, which performed active twisting of the free end of their body for a long time, were not wrapped until about 10 min after capture. Very

large, single prey were wrapped only after a lengthy period, 1 hr or more, had elapsed. It appears that the absence of vigorous movements by the prey is a necessary part of the stimulus situation for the onset of wrapping.

Post-immobilization wrapping in other wandering spiders. — Our two species of *Lycosa* performed post-immobilization wrapping, whereas *Schizocosa crassipes* did not. We modified our original speculation that this behavior might be characteristic of the Lycosidae to the notion that it might be at least genus-specific. Even this is no longer tenable, in light of our preliminary observations on other species as well as data obtained by R. J. McKay (personal communication). We now regard post-immobilization prey-wrapping as a behavioral adaptation that may be included in the repertoire of various unrelated wandering spiders that have specialized for spending part or most of their time some distance above the ground on vegetation.

Post-immobilization wrapping occurs after the prey has stopped struggling, occupies a relatively brief amount of time during the lengthy feeding process, and is used for prey only when the total volume exceeds some threshold value. These are the probable reasons why this behavior has not yet been reported in many species in which it is likely to occur. Authors specifically studying feeding behavior have seen post-immobilization wrapping in two other families of wandering spiders — ctenids (Melchers, 1961, 1963) and theraphosids (Eberhard, 1967), although neither of these authors determined the function.

A personal communication from E.-A. Seyfarth, that wrapping occurred in *Cupiennius salei,* called our attention to the work of Melchers (1961, 1963) on this ctenid species. (Comparison with our species was facilitated by our being able to view Melchers' (1961) film of this behavior.) Post-immobilization wrapping by *C. salei* is very similar to what occurs in our *Lycosa* spp. as to the sequence of events and movements, stimuli releasing the behavior, etc. However, two differences are obvious: (1) *C. salei* waits for prey on a vertical surface. If it tumbles to the ground during prey capture, it carries the prey back up to an elevated point on the vertical surface — the glass wall of the terrarium in Melchers' study. Individuals of our species never did the latter, but readily stayed on the ground to feed if the capture ended there. (2) The density and breadth of the swathing bands are much greater in *C. salei* than in our *Lycosa* spp. Points 1 and 2 are probably interrelated and suggest that this ctenid

spider is even more specialized for living on vegetation than are our *Lycosa* spp.

Scopula hairs, which enable spiders to climb smooth surfaces, have been studied in lycosids, theraphosids, and other wandering spiders (Foelix and Chu-Wang, 1974). Since these structures are an important adaptation for many of the spiders which spend their life on vegetation, they may serve as a morphological indicator of behavioral correlates of this life style, including post-immobilization prey-wrapping. Indeed, a scopula is present in those species in which this behavior has been seen. On the other hand, since scopula hairs on the tarsus and metatarsus are probably important for the capture and manipulation of prey (Rovner and Knost, in preparation), their presence may not always be indicative of habitat preference and related behaviors.

Experimentally modified male *L. rabida* that are unable to achieve palpal insertions "tie-down" females during attempted copulation (Rovner, 1971), a behavior resembling post-immobilization wrapping of large prey. Male thomisid spiders perform a similar behavior as part of their normal pre-copulatory activity. (In neither case does the wrapping have any restraining effect on the female, who easily tears the threads and departs when the copulation is completed.) Perhaps the pre-copulatory wrapping in thomisids is a ritualized behavior derived from a present or past use of silk for wrapping prey in this family.

Eberhard (1967) associated post-immobilization wrapping with certain primitive types of aerial web-building, similar to that exhibited by the present-day diguetid spiders. The behavior shown by our *Lycosa* spp. of the herbaceous stratum, and by other wandering spiders, suggests that the evolution of post-immobilization wrapping may not be as closely associated with the building of aerial webs as Eberhard had hypothesized.

Summary

Post-immobilization wrapping of large, single prey and groups of smaller prey occurs in *Lycosa rabida* and, to a lesser extent, *Lycosa punctulata.* Observation of these spiders in both the natural habitat and an artificial habitat indicated their preference for the herbaceous stratum. Post-immobilization wrapping is probably an adaptation for life in this stratum, since it reduces the possibility of losing prey when it is released from the cheliceral grasp. The swathing bands, attachment disks, and draglines involved in wrapping are produced

with silk from the aciniform, piriform, and ampullaceal glands respectively. Post-immobilization prey-wrapping, well-known in web-weavers and now known in ctenids, lycosids, and theraphosids, is likely to be found in other wandering spiders that live on foliage.

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ERRATUM. — In our paper on "Social Carrying Behavior and Division of Labor During Nest Moving in Ants", *Psyche,* Vol. 81, No. 2, pages 219-236, the last line of the caption of Fig. 10 should read: Dotted Line: *Formica sanguinea;* Solid Line: *Camponotus sericeus.* — Michael Möglich and Bert Holldobler (Biological Dept., MCZ-Laboratories, Harvard University).

PTERALIA OF THE PALEOZOIC INSECT ORDERS PALAEODICTYOPTERA, MEGASECOPTERA AND DIAPHANOPTERODEA (PALEOPTERA)*

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For an understanding of insect evolution the structure of the wing base is of major significance. However, the fossil record of pteralia in extinct orders is extremely scanty. This paper is concerned with the wing bases of certain Paleozoic Paleoptera, namely, Palaeodictyoptera, Megasecoptera and Diaphanopterodea from the Upper Carboniferous (Namurian) of Czechoslovakia, the Upper Carboniferous (Stephanian) of France, and the Lower Permian of Czechoslovakia and Kansas. Independently of the Neoptera, the Diaphanopterodea acquired the ability to flex the wings backwards over the abdomen. In this respect, the order is of special interest, and an attempt is made here to compare the pteralia of the Diaphanopterodea with those of extant Ephemeroptera.

Our present knowledge of the wing base in Paleozoic Paleoptera is restricted to the axillary plate of several palaeodictyopteran adults (Kukalova, 1960, 1969-70), and palaeodictyopteran nymphs (Wootton, 1972; Sharov, 1971) [See figures 1, 2 and 4]. Recently, the wing base has been described in the Diaphanopterodea, Family Elmoidae (Kukalova-Peck, 1974) (fig. 8). In the present paper, the axillary plates in Martynoviidae and Asthenohymenidae of the Order Diaphanopterodea are included, and for the first time the axillary sclerites in Megasecoptera are described.

The interpretation and terminology of the pteralia in extinct Paleoptera are necessarily dependent upon the detailed functional morphology of extant Ephemeroptera and Odonata. At the same time, the wing base structures found in extinct orders provide an evolutionary view and might be helpful in unraveling the enigmatic archi-

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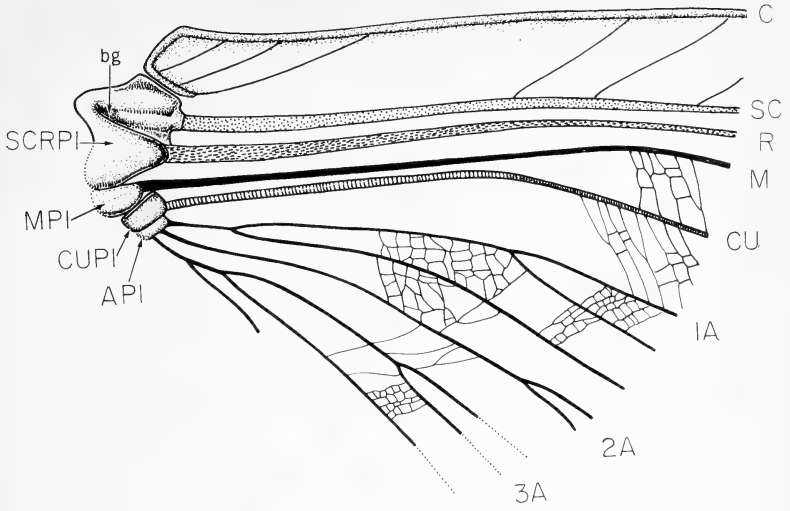

Fig. 1. Partially fused axillary plate of *Boltopruvostia nigra* (Palaeodictyoptera, Homoiopteridae). Enlarged base of fore wing. Redrawn from Kukalova, 1960. APl — anal plate; bg — basal groove; CuPl — cubital plate; MPl — median plate; ScRPl — subcosto-radial plate. Upper Namurian, Czechoslavakia.

tecture of extant Paleoptera. In the Odonata, the thorax and pteralia have been discussed in detail by Tannert (1958), Neville (1960), and Hatch (1966), but interpretation of these structures is still subject to debate. The axillary plate is considered either as the fused radio-anal plate, or as a compound structure, with the radio-anal plate, axillary sclerites, and subalare incorporated. However, the wings of the Odonata are highly specialized and possess many unique features and therefore are less suited for comparison with Paleozoic orders than the more primitive wings of the Ephemeroptera. The pteralia in Ephemeroptera have been recently studied by Brodskyi (1970), Matsuda (1970), and Tsui and Peters (1972) (fig. 5), but the axillary plate was not described in functional terms; it was mostly referred to as "median plate". In this paper, the terminology is derived from Tannert's (1958) account on the Odonata and the respective axillary plates are called by the terms of incorporated basal plates of the veins. Since the fossil specimens do not contribute to our knowledge of whether the other pteralia are fused with the axillary plate, this problem should be considered as fully open to future emendations based upon a detailed study of functional morphology.

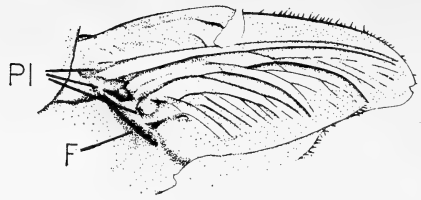

Fig. 2. Palaeodictyopteran nymphal wing pad with partially separate basal plates. *Idoptilus onisciformis* (Graphiptilidae). After Wootton, 1972. F — deep furrow along the thorax; Pl — basal plates. Westphalian, England.

Palaeodictyoptera and Ephemeroptera

In the most primitive, yet unknown, Paleoptera all main veins probably originated at the wing base from the separate basal plates. In the process of evolution, the basal plates gradually became fused. The intermediate stage of partial fusion is documented in the primitive palaeodictyopteron, *Boltopruvostia nigra* (Namurian C of Czechoslovakia, fig. 1). In this species the subcostal and radial plates are fully grown together (forming the subcosto-radial plate), the median plate is separate, and the cubital plate is fused with the small anal plate (forming the cubito-anal plate). The partially separated basal plates are also indicated in the wing pad of the nymph *Idoptilus onisciformis* (Wootton 1972, Westphanian of England) (fig. 2).

Within the evolutionary history of Palaeodictyoptera, full fusion of the plates was acquired in the more specialized forms. Basal plates fused together into a single subcosto-anal plate but still retaining an indication of individual outlines, have been found in *Moravia convergens* (Lower Permian of Czechoslovakia, fig. 3). In Palaeodictyoptera from the Upper Carboniferous of France (fig. 4), the subcosto-anal basal plate is fully fused and its subcostal part becomes reduced in size.

In the primitive Ephemeroptera (Siphlonuridae, fig. 6), the costal brace in the fore wing starts at the anteroproximal angle of the axillary plate; in the hind wing, it sometimes starts from a transverse elevation on the axillary plate, forming a convex hook directed against the stem of M. The costal brace is, in all probability, homologous to the postcostal vein of Palaeodictyoptera (fig. 4B, pv), plus the cross vein between Sc and R. The base of ephemeropteran wings is weakly sclerotized and the stems of the main veins adjacent to the axillary plate are mostly not discernible. However, if the vein stems

in primitive mayflies are thoroughly examined, their connection with the axillary plate can be traced. This is true in many Siphlonuridae, especially in the hind wings (fig. 6B). In the fore wing of *Siphlonurus mirus* (fig. 6A), the axillary plate is domed in the middle. At the anteroproximal angle, there is a short groove, which is also present in Palaeodictyoptera (fig. 1, 3). Expanded stems of Sc and R (which might in this *Siphlonurus* be represented by the fused R + M + Cu stems) meet at a suture and clearly penetrate the axillary plate. In the hind wing of the same species, the groove at the anteroproximal angle is reduced to a small pit. R is located at the anterior part of the dome and is closely followed by the short stem of M, from which MA and MP diverge almost immediately. The short stem of Cu

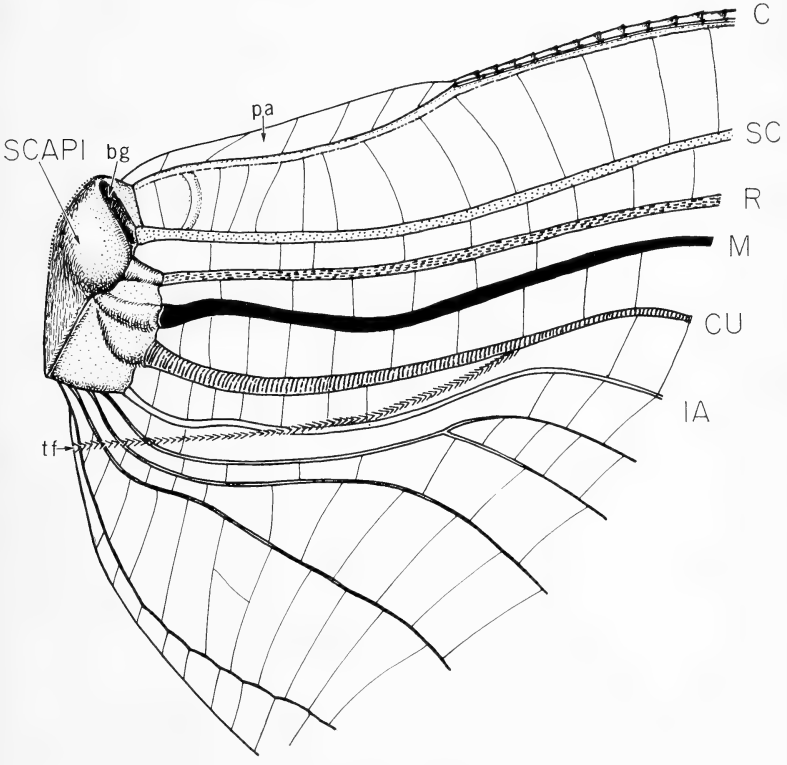

Fig. 3. Fused subcosto-anal plate of *Moravia convergens* (Palaeodictyoptera, Calvertiellidae). Enlarged base of the fore wing. Original. bg — basal groove; pa — precostal area; ScAPl — subcosto-anal plate; tf — transverse furrow. Lower Permian, Czechoslovakia.

meets MP and instantly splits into CuA and CuP. As described above, all main veins, with the exception of the anal veins, start in the hind wing directly and separately from the domed part of the axillary plate, as in more advanced Palaeodictyoptera (fig. 4).

The main difference between the axillary region of the Palaeodictyoptera and that of the Ephemeroptera is in the attachment of the anal veins. In the Palaeodictyoptera, the anal veins probably always originated directly from the subcosto-anal plate (figs. 3, 4), or the anal plate was closely attached to the cubital plate (fig. 1). The anal area in Palaeodictyoptera is often crossed by diverse convex ridges, which are sometimes V-shaped (*Homaloneura,* Kukalova 1969), and by transverse grooves (figs. 3, 4A), or the anal veins start from a cuticular thickening (*Dunbaria,* Kukalova-Peck 1971). As pointed out by Wootton (1974, personal communication), these structures are in the place of the anal brace of Ephemeroptera. In the primitive mayflies, the anal veins start at the anal brace, which is basally attached to a small plate, separated from the large axillary plate. It seems possible that while the axillary plate originated by fusion of the subcosto-cubital plates, the anal plate stayed detached. This condition is partially reminiscent of Diaphanopterodea and Megasecoptera, as will be shown below. The anal brace in Ephemeroptera is followed, both anteriorly and posteriorly, by two concave furrows. By location and, very probably, by function for flight, the furrows may be compared with the concave transverse furrow, crossing the anal area in almost all Palaeodictyoptera (figs. 3, 4A).

The weak sclerotization of the axillary plate in Ephemeroptera and the vanishing of the adjacent stems are probably the changes which

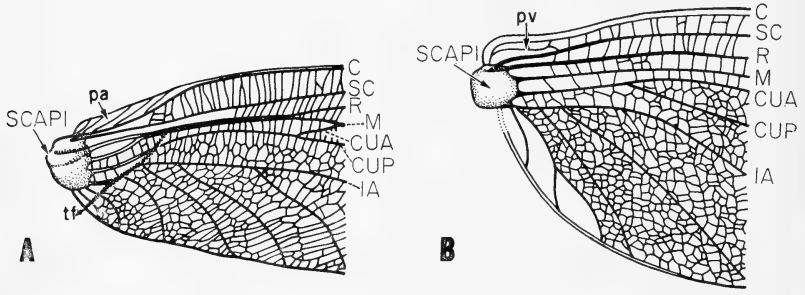

Fig. 4. Fused subcosto-anal plates of Palaeodictyoptera. A. *Dictyoptilus sepultus* (Eugereonidae), enlarged base of the fore wing. B. *Stenodictya parisiana* (Dictyoneuridae), enlarged base of the hind wing. After Kukalova, 1970. pa — precostal area; pv — postcostal vein; ScAPl — subcosto-anal plate; tf — transverse furrow. Upper Carboniferous, France.

occurred later in evolution. This conclusion is supported by the morphology of primitive Permian mayfly families, the Protereismatidae and the Misthodotidae. In both, the stems of main veins were strong, reaching the wing base, and the anal brace was less pronounced than in extant mayflies (fig. 7). It should be noted that the adult life span in Permian Ephemeroptera was probably longer than in Recent species; the presence of large and apparently fully functional mouthparts in the adult Permian Misthodotidae (Tschernova, 1965) is very suggestive that these particular mayflies, at least, were active feeders. Flight was presumably important in obtaining food, as well as in courtship activities.

According to Brodskyi (1970), the second axillary sclerite in Recent Ephemeroptera is firmly fused with the axillary plate, although this opinion is not shared by some other specialists; the schematic figure of the axillary region in extant mayflies (Leptophlebiidae) in the interpretation of Tsui and Peters (1972) is shown in figure 5. In the fossil material described, no remnants of the axillary region have been mentioned so far.

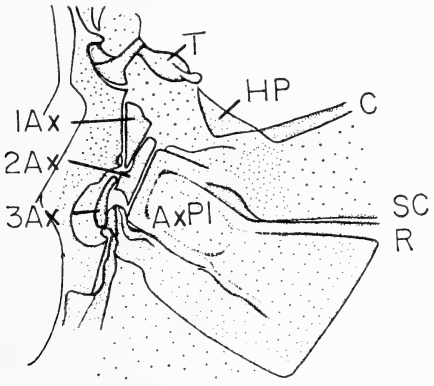

Fig. 5. Axillary region of fore wing of ephemeropteron, *Aprionyx tricuspidatus* (Leptophlebiidae, adult male). After Tsui and Peters, 1972. AxPl — axillary plate; Ax 1, 2, 3 — axillary sclerites; HP — humeral plate; T — tegula. Recent.

Diaphanopterodea

The Diaphanopterodea have mouthparts, genitalia and wing venation pattern very similar to those of Palaeodictyoptera, from the primitive forms of which they were probably derived (Carpenter,

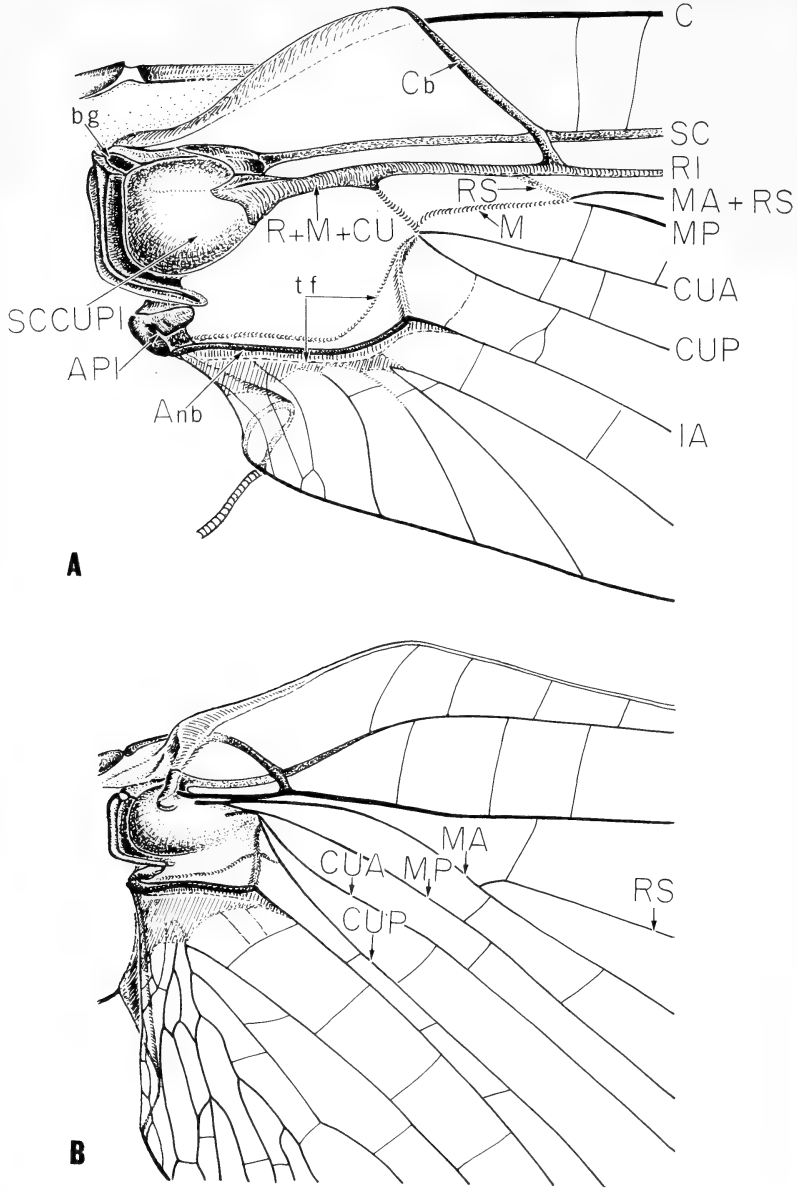

Fig. 6. Subcosto-cubital plate of ephemeropteron, *Siphlonurus mirus* (Siphlonuridae). A. Fore wing; B. Hind wing. Original. Anb — anal brace; APl — anal plate; bg — basal groove; Cb — costal brace; ScCuPl — subcosto-cubital plate; tf — transverse furrow. Recent.

1963). In comparison with the average size of Palaeodictyoptera, they are much smaller and they developed the ability to flex the wings backwards over the abdomen. The axillary plate of the wing base and the basal fold were recently described by Kukalova-Peck (1974) in *Permodiapha carpenteri* of the family Elmoidae (fig. 8A). Here, the axillary plate is compared with that of the related family Martynoviidae as preserved in *Martynovia protohymenoides* (specimen No. 4600, Museum of Comparative Zoology, Harvard University) from the Lower Permian of Kansas (fig. 8B).

In both forms, the general patterns of the wing base structure are similar. The larger part of the axillary plate in *Martynovia* is formed by the fused medio-cubital plate, or perhaps by the cubital plate itself. Different is the development of the anal plate, which is distinctly outlined and two-lobed, located anteriorly to the basal fold. The anal plate is firmly connected by the anterior margin with the axillary plate. The basal fold encircles the axillary plate anteriorly and distally and separates it from the sclerotized region, extending between CuP and the posterior wing margin (fig. 8B, S). The axillary plate in both *Martynovia* and *Permodiapha* is obliquely crossed by a convex strut, which perhaps participated in the folding of the wings. The incompletely preserved axillary sclerite contacts

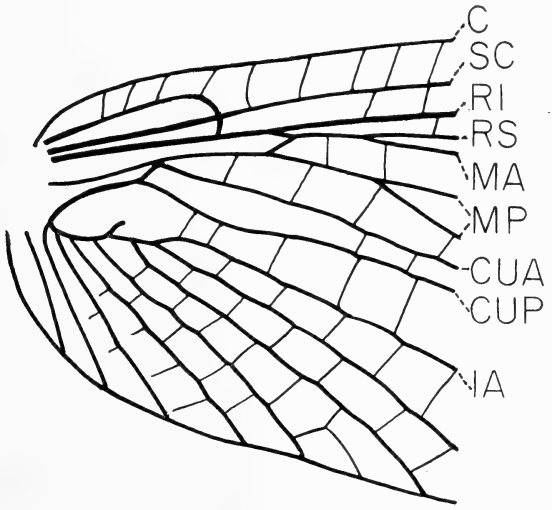

Fig. 7. Fore wing base of Permian mayfly, *Protereisma permianum* (Protereismatidae). After Carpenter, 1933. Lower Permian, Kansas.

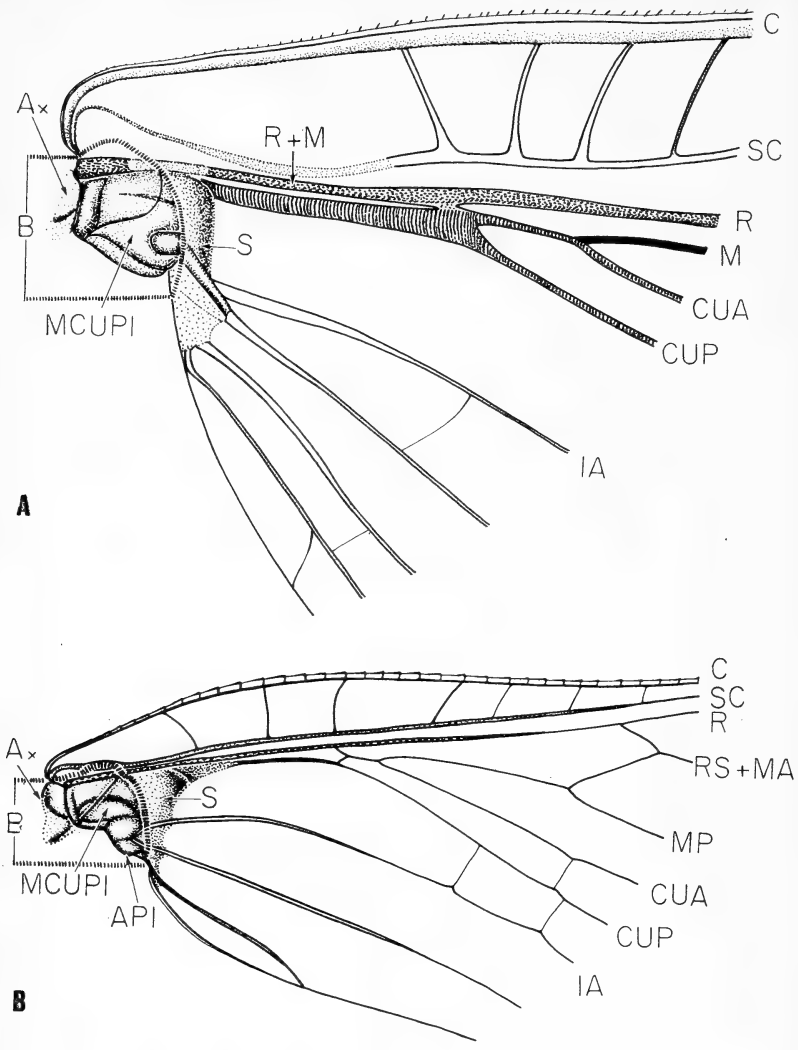

Fig. 8. Medio-cubital plate of Diaphanopterodea. A. *Permodiapha carpenteri* (Elmoidae), hind wing. After Kukalova-Peck, 1974. B. *Martynovia protohymenoides* (Martynoviidae), fore wing. Original. APl — anal plate; Ax — axillary sclerite; B — basal fold; MCuPl — medio-cubital plate; S — sclerotized region. Lower Permian, Czechoslovakia and Kansas.

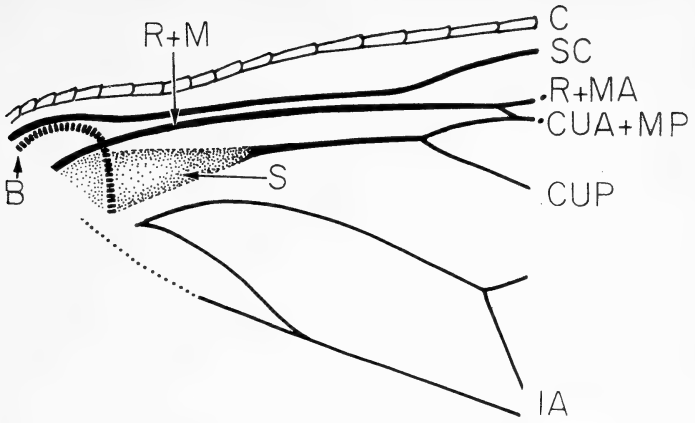

Fig. 9. Incomplete wing base of *Asthenohymen dunbari* (Diaphanopterodea, Asthenohymenidae). Fore wing. Original. B — basal fold; S — sclerotized region. Lower Permian, Kansas.

with the proximal margin of the axillary plate and with R. It is in the position of 2 Ax in Recent Ephemeroptera (*sensu* Tsui and Peters 1972, fig. 5).

In Asthenohymenidae, the incompletely preserved wing base, including only the basal fold and part of the sclerotized region, is known. The structure of the wing base, as preserved in *Asthenohymen dunbari* (specimen No. 3835, Museum of Comparative Zoology, fig. 9) seems to be basically similar to that of *Martynovia* and *Permodiapha.*

The fused axillary plate of Diaphanopterodea is homologous only to the posterior part of the subcosto-anal plate of Palaeodictyoptera. The subcostal, radial, and possibly also the median basal plates became completely reduced, perhaps in connection with narrowing of the wing base, coalescence of veins and with acquisition of wing folding ability.

Megasecoptera

The Megasecoptera and Palaeodictyoptera have very similar mouthparts, genitalia and wing venation pattern, and undoubtedly developed from common ancestral stock. The Megasecoptera differed, according to our previous understanding, only in the shape of the wings and in the more pronounced crowding of Sc and R towards the costal margin. However, the study of the wing base has revealed a

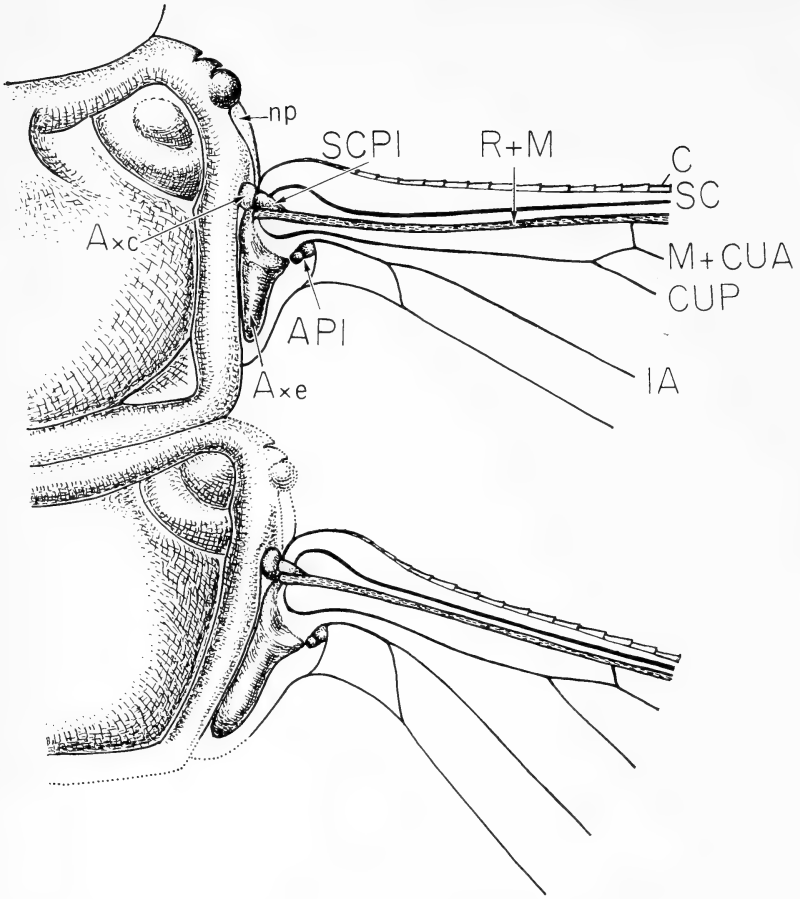

Fig. 10. Pteralia of *Protohymen permianus* (Megasecoptera, Protohymenidae). Enlarged base of the fore and hind wings. Original. API — anal plate; Axc — convex axillary sclerite; Axe — elongated axillary sclerite; np — narrow plate; ScPl — subcostal plate. Lower Permian, Kansas.

major difference in the pteralia, not only with respect to Palaeodictyoptera, but also to all other paleopterous orders.

The well preserved wing bases with axillary sclerites were found in specimens of two comparatively small species: *Protohymen permianus* (specimen No. 3060) and *Protohymen readi* (holotype No. 3258), in the Museum of Comparative Zoology. Since the structures in both specimens are similar, only the wing bases of *Protohymen permianus,* which is better preserved, are described (fig. 10).

Towards the base, the wing narrows markedly in the posterior part, while the anterior margin remains almost straight. Shortly before the base, the posterior margin curves posteriorly to form a prolonged axillary lobe parallel with the tergal margin. The serrated costa is attached at the very base to a long narrow plate on the lateral margin of the tergum. This plate is connected anteriorly with a prominent, darkly colored lobe. The subcosta is convexly bent near the base. Both costa and subcosta terminate on a triangular, highly convex basal plate, which is posteriorly connected to R + M and proximally to the small, convex axillary sclerite. This is associated with the tergal margin, the basal plate, the costa, the narrow plate on the tergum, and the anterior arm of the large elongated sclerite. The cubitus is concavely bent towards the very end of R shortly before the base, so that it creates the mirror image of the subcosta. The anal vein originates from a small anal plate, which is divided by a perpendicular suture into two small equal sections. The anal plate is directed obliquely and posteriorly against the posterior arm of a large, anteroposteriorly elongated sclerite. This closely contacts the tergum along almost its entire proximal margin. The elongated sclerite is highly convex posteriorly from the level of the end of the anal plate. In the anterior, flatter part, the axillary sclerite divides into two arms. The proximal arm is longer and slightly bent to attach to R + M and to the small axillary sclerite; the distal arm is shorter and directed to connect the curved end of the anal plate. This sclerite is markedly larger in the hind wing.

The megasecopteran pteralia, as described above (figs. 10, 11), are so highly specialized that homology at our present level of knowledge is nearly impossible. The narrow plate laterally on tergum (np) and the elongate sclerite (Axe) as well seem to be compound structures in which several elements might be incorporated. The small convex sclerite (Axc) is approximately in the position of 1Ax of Ephemeroptera (*sensu* Tsui and Peters 1972; fig. 5). The little basal plate (ScPl) at the beginning of Sc is perhaps homologous to the subcostal basal plate of hypothetical primitive Paleoptera. The highly specialized character of megasecopteran pteralia shows that the construction of the wing attachment in Paleoptera was even more varied and diverse than it has been assumed. However, it should be taken into consideration that the pteralia of *Protohymen* may not be typical for the whole order Megasecoptera because of its relatively small size. In small insects, reduction and other modification of axillary sclerites sometimes occur.

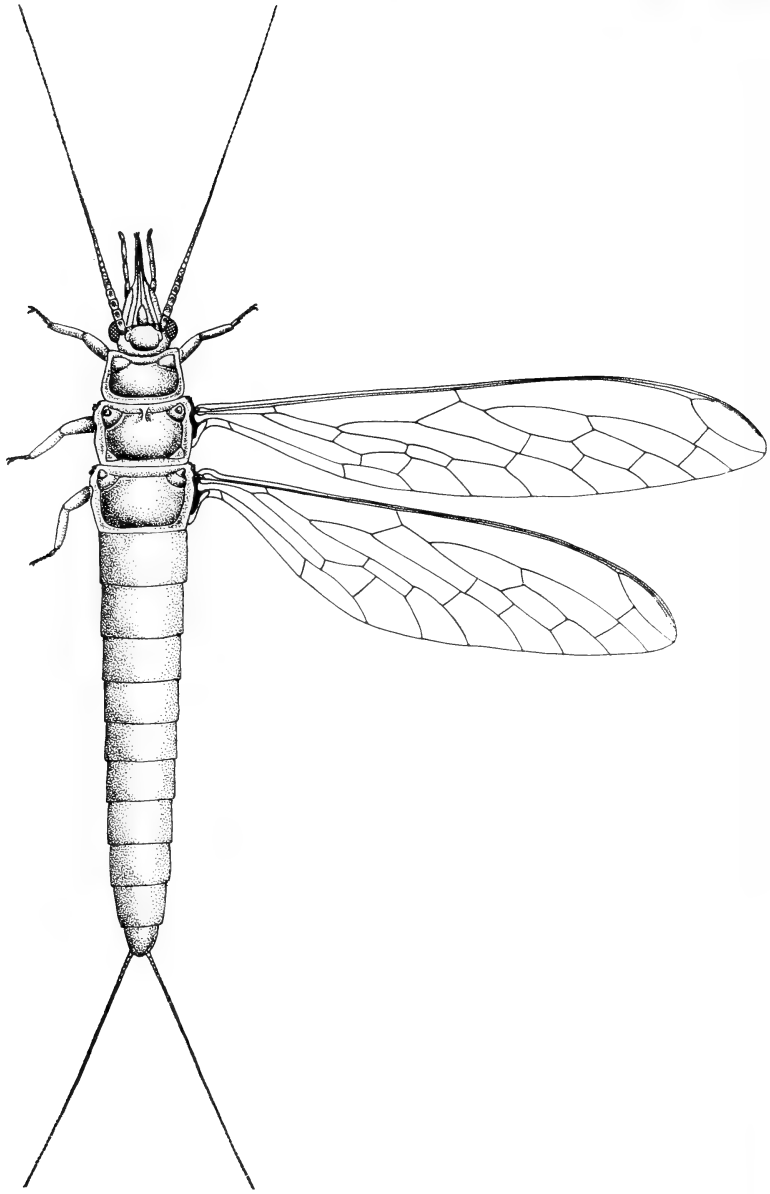

Fig. 11. Reconstruction of *Protohymen* (Megasecoptera, Protohymenidae). All structures shown are preserved in specimens of *Protohymen permianus* and *P. readi,* except for the meso- and metathoracic legs, which are restored on the basis of the prothoracic legs. Original. Lower Permian, Kansas.

Summary

In the several paleopterous orders, the "axillary plates" are by no means to be considered as fully homologous structures. They are formed by fusion of various basal plates, which can eventually vary in the degree of fusion and in the individual size within a single order (for instance in Palaeodictyoptera, and in Diaphanopterodea).

There is little doubt that in the hypothetical primitive ancestor of Paleoptera the main veins originated from the separate basal plates. From this condition, the axillary plate was derived by fusion of the following plates: in Palaeodictyoptera, of subcosto-anal plates; in Ephemeroptera, of subcosto-cubital plates; in Odonata, of radio-anal plates; in Diaphanopterodea, of medio-cubital plates; in Megasecoptera, only small subcostal plate remained.

In spite of the variability mentioned above, the general plan of the axillary region and adjacent part of the wings is shared by all paleopterous orders, and certain structures, functionally significant for the flight, repeat many times throughout Paleoptera. For instance, separated or semi-separated anal plates occur in Magasecoptera, Diaphanopterodea, and Ephemeroptera. A deeply concave furrow crossing transversely the anal area is found in almost all Palaeodictyoptera and in the Ephemeroptera. Transverse reinforcement of the proximal half of the wing formed by coalesced veins and supporting cross veins, cuticular thickenings and pigmented stripes is present in Odonata and in "odonatoid" (dragonfly-convergent) Palaeodictyoptera, etc. These structures will not be understood until more study of the functional morphology has been done, particularly on extant mayflies, dragonflies, and on wings in general.

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SYSTEMATICS OF THE TRAPDOOR SPIDER GENUS *ALIATYPUS* (ARANEAE: ANTRODIAETIDAE)*

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Introduction

Aliatypus species are all rather stocky mygalomorph spiders (Figs. 45-49) which construct a burrow with a trapdoor entrance from which they capture prey. In general morphology and behavior, *Aliatypus* bears striking resemblance to the distantly related trapdoor spider family Ctenizidae, but this similarity is clearly the result of convergent, or at least parallel, evolution; *Aliatypus* is an atypoid mygalomorph taxon most closely related to *Antrodiaetus, Atypoides,* and the Mecicobothriidae. *Aliatypus* species appear to be restricted to California and Arizona (Maps 1-4) where they live in ravine banks, road banks, or other slopes in habitats ranging from hot, dry sagebrush scrub communities to wet coast redwood forests and cool California red fir mountain forests. They are among the most abundant trapdoor spiders in California.

Aliatypus has been badly neglected; only one species has been described (Banks, 1896; Smith, 1908) and little natural history information has been published (Smith, 1908; Gertsch, 1949; Coyle, 1971). During the last seven years a concerted collecting effort, largely by Wendell Icenogle and myself, has increased the availability of adult specimens from a dozen to 330 and has thereby made possible this revision. My chief goal in this study has been to define accurately the species limits by means of an analysis of variation. The methods employed are essentially those of my earlier studies (Coyle 1968, 1971) and are summarized in the Methods section of this paper. Discussions of variation patterns are included in order to improve our understanding of geographic variation in mygalomorph spiders and guide future research on *Aliatypus.* The considerable amount of behavioral and ecological data which has been collected will be published separately in a paper on *Aliatypus* natural history.

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I hope that these studies of *Aliatypus* will stimulate others to investigate these fascinating spiders. Considerably more collecting is necessary before *Aliatypus* systematics can be confidently understood. As pointed out in the discussions of variation, small sample sizes and sizeable geographic gaps from which no samples are available have greatly limited the strength of some of my conclusions. The variation discussions, locality records, and distribution Maps 2-4 (Map 4 marks the distribution of unidentifiable *Aliatypus* specimens.) should help direct future collecting efforts.

Acknowledgements

Willis Gertsch first recognized the potential diversity within *Aliatypus* and suggested that I revise the genus. Wendell Icenogle deserves tremendous credit for the hours he labored collecting about 55 percent of the specimens upon which this study is based. He was the first collector of five new species. Without his field work this study would be very incomplete. Jim Horton, my department head during most of this research, provided needed space and release time. I thank the following individuals and institutions for loans of *Aliatypus* specimens: William Azevedo, Michael Bentzien, Patrick Craig, Willis Gertsch (American Museum of Natural History), Wendell Icenogle, Herbert Levi (Museum of Comparative Zoology), Patrick Marer, Robert Schick (California Academy of Sciences), and Mel Thompson. This research and its publication have been supported by a grant (GB-34128) from the National Science Foundation.

Evolution

PHYLOGENY

Aliatypus, Antrodiaetus, Atypoides, the Mecicobothriidae, and the Atypidae form a distinct monophyletic taxon (Coyle, 1971). *Aliatypus* is probably an old group, so that the details of its relationship to these other atypoid mygalomorph taxa are not now clear. The question of whether *Aliatypus* is more closely related to *Antrodiaetus* and *Atypoides* or to the mecicobothriids was discussed earlier (Coyle, 1971), but will remain unresolved until after the completion of a careful comparative study of all atypoid mygalomorphs.

In Figure 1 I have presented a hypothetical phylogeny of the genus *Aliatypus*. This speculation is based upon a comparison of character states in living *Aliatypus* species and related genera. It is

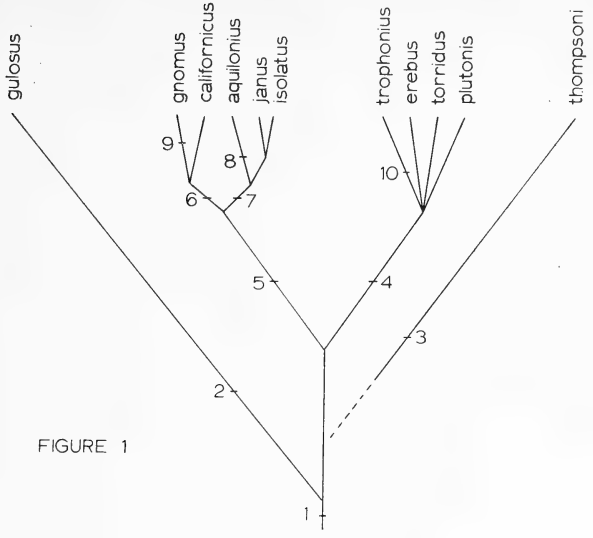


FIGURE 1

Figure 1: Suggested phylogeny of *Aliatypus* species. 1. Character states of hypothetical ancestral stock: No ICS keel or OCS keel. Seminal receptacles with moderately long, sinuous, non-tapering stalks and medium sized bulbs. Posterior sigilla small and well separated. Legs of moderate length. Thoracic groove a deep pit. Leg I setation as in majority of species. Moderately large body. 2. Seminal receptacle stalks become short and straight. Legs become proportionately shorter. 3. Posterior sigilla enlarge. Thoracic groove lost. Leg I setation changes. 4. Posterior sigilla enlarge. Legs become proportionately shorter. Become adapted to dryer habitats. 5. Become adapted to more humid and cooler habitats. 6. ICS keel develops. 7. Seminal receptacle stalks become tapered. 8. Conductor tip changes form. Body size reduced. 9. Seminal receptacle stalks become less elongate and less sinuous. Body size reduced. 10. Body size reduced.

meant to be a useful working hypothesis, subject to revision. Characters which were relied upon most heavily are palpus form, seminal receptacle form, and posterior sigilla size and placement. The actual direction of evolution in some characters may well be the reverse of those suggested. It is certain that *Aliatypus* contains two distinct groups of closely related species — *A. californicus, A. janus, A. isolatus, A. aquilonius,* and *A. gnomus* on the one hand and *A. trophonius, A. erebus, A. plutonis,* and *A. torridus* on the other — and two distinct species, *A. gulosus* and *A. thompsoni,* each rather distantly related to all the others.

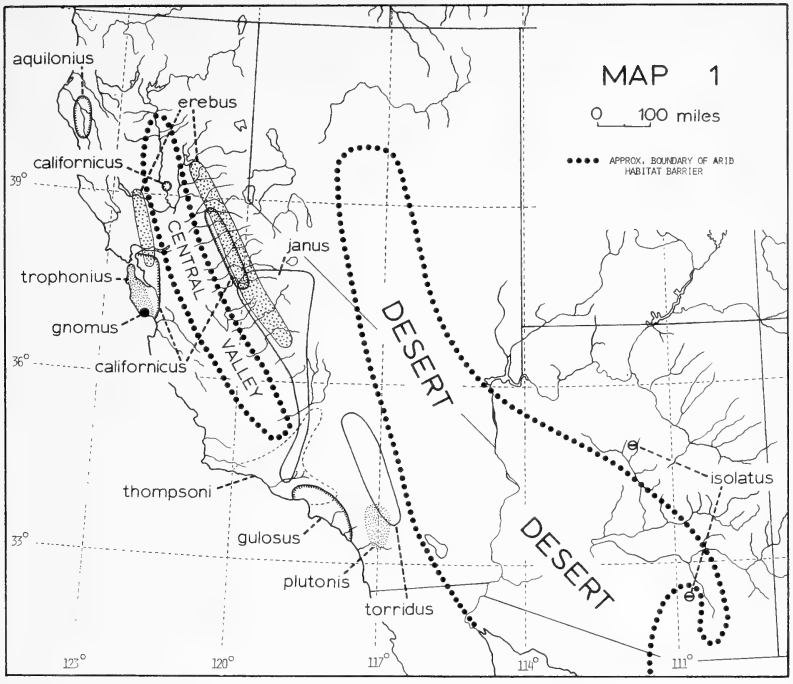
GEOGRAPHIC VARIATION AND SPECIATION

As is the case in *Antrodiaetus* (Coyle, 1971), *Atypoides* (Coyle, 1968), and probably most other burrowing mygalomorph genera (See, for example, Main, 1957; Loksa, 1966; and Forster and Wilton, 1968.), there is considerable geographic variation in some species of *Aliatypus*. Detailed descriptions of these geographic variation patterns can be found in the Taxonomy section. My purpose here is to consider some of the causes of these patterns.

The environmental tolerance ranges and dispersal ability of a species are key factors in determining what environmental conditions constitute barriers which can fragment and isolate its populations so that genetic divergence can take place. Little pertaining specifically to *Aliatypus* dispersal can be added to my earler discussion of dispersal ability in antrodiaetids (Coyle, 1971). In summary, the probability of successful colonization of distant localities by long distance aerial dispersal is extremely low; aquatic rafting, short distance spiderling dispersal, and male wandering are probably the only important means of dispersal under natural conditions. As in *Antrodiaetus* and *Atypoides,* environments with very low humidity, such as deserts or semiarid grasslands, are the outstanding barriers to dispersal and thus gene flow in *Aliatypus*. However, some species of *Aliatypus,* notably *A. plutonis* and *A. torridus,* are less well restricted by dry barriers than are most other antrodiaetids.

The following discussions, although partly speculation, should, like any working hypotheses, help direct further research. Frequent referral to Map 1 will help to understand them.

The Central Valley of California, a semiarid grassland in its recent natural state, appears to be a strong barrier to gene flow between coastal and Sierran populations of both *Aliatypus californicus* and *Aliatypus erebus*. The genetic discontinuity between these populations may even be great enough to merit calling them incipient species. A similar situation exists in *Atypoides riversi* (Coyle, 1968 and 1971). Apparently, during Pleistocene glacial periods when the climate was wetter and cooler, dispersal of these species occurred across favorable wooded parts of the Central Valley. The recent discovery of isolated *A. californicus* and *A. riversi* populations in the Sutter Buttes of the Central Valley indicates that this was once part of such a corridor allowing gene flow across the valley. Similar dispersals across the Central Valley during Pleistocene glacial periods are also indicated by distribution patterns of the salamander genera *Ensatina* and *Taricha,* which, like *Aliatypus,* require rather mesic habitats (Stebbins, 1949; Riemer, 1958). I suspect that the antro-



Map 1. Known distribution ranges of *Aliatypus* species in relation to present major arid habitat barriers which formed during the retreat of the Wisconsin glaciation.

diaetid trans-valley connections existed during the most recent (Wisconsin) glacial period and consequently became severed as recently as 13,000 years ago. Perhaps the *A. californicus* population at Mariposa, which is phenotypically more distinct from the coastal population than is the north Sierran population, was last connected with the coastal population during an earlier glacial period; or perhaps its trans-valley connections were simply severed earlier during the retreat of the last (Wisconsin) glacial period than were those of the north Sierran populations. Perhaps continued expansion of habitat barriers during the present post-glacial period has tended to restrict gene flow between the morphologically divergent northern populations of *A. erebus* and its south Sierran populations.

There is much geographic variation in *Aliatypus janus,* but the samples are so small and scattered that it is difficult to recognize important barriers to gene flow. The northernmost samples probably

represent the kind of semi-isolated, genetically divergent, peripheral populations found in many species. *Aliatypus thompsoni* variant populations are also at the periphery of the species range, where suitable habitats are probably uncommon and semi-isolated. The Tehachapi Mountains apparently provide (or recently provided) an east-west corridor of favorable habitats for the dispersal of *A. janus* and *A. thompsoni* between the southern end of the Sierra Nevada Mountains and the coastal mountain ranges. The morphologically divergent nature of the *A. thompsoni* samples at Tehachapi and in the southern end of the Sierra Nevada Mountains indicates that this corridor is not currently supporting much dispersal.

The phenotypic differences between the two known *Aliatypus isolatus* populations in Arizona are almost certainly caused by the disruption of gene flow after the recent (Wisconsin) glacial period as desert and grassland barriers expanded all over the Southwest to isolate various mesic mountain habitats. Pollen analyses (Martin and Mehringer, 1965) demonstrate that during the Wisconsin glacial period (which apparently lasted in that area until about 13,000 years ago), woodland and forest habitats favorable for *A. isolatus* extended continuously throughout western and northern Arizona. Thus the similar geographic variation patterns in *A. isolatus* and *Antrodiaetus apachecus* (Coyle, 1971) probably have a common cause.

The extreme similarity of allopatric *Aliatypus janus* and *Aliatypus isolatus,* when viewed with Southwest pollen analyses (Martin and Mehringer, 1965) in mind, leads to the conclusion that these two species were formed when a recent interglacial expansion of the Sonoran and Great Basin Deserts severed a previously widespread ancestral population. Convincing evidence that 17,000 to 23,000 years ago (during the Wisconsin glacial period) woodland extended continuously from current *A. isolatus* localities to the present range of *A. janus,* strongly indicates that these sister species may be only 15,000 years or so old. Indeed, it is possible that genetic divergence has not even progressed far enough for the development of reproductive isolating mechanisms.

There are three other pairs of closely related *Aliatypus* species — *A. janus* and *A. aquilonius, A. californicus* and *A. gnomus,* and *A. erebus* and *A. trophonius* — which are not as similar as *A. janus* is to *A. isolatus.* It is possible that each of these pairs originated from a trio of ancestral species fragmented by arid barriers, such as the present Central Valley, during an earlier Pleistocene interglacial. Interestingly, each of these pairs consists of a large and a small species.

Methods

COLLECTING METHODS

Because of their covert behavior, *Aliatypus* spiders are rarely collected except when one concentrates on special collecting strategies. Banks and slopes of promising habitats (to be described thoroughly in a paper on *Aliatypus* natural history) are best searched in daylight by carefully examining suitable microhabitat surfaces for the outline of a closed trapdoor. However, whenever the trapdoors are sealed, such as during dry periods, they may become covered with loose soil particles or other debris; carefully shaving away the top layer of soil may then be the only way to locate burrows. Night collecting is usually less satisfactory than daytime collecting since even unsealed *Aliatypus* doors are only cracked open at night and not easily located with artificial light. At night it is sometimes possible to trap active spiders at their burrow entrances by thrusting a knife blade into the soil and across the burrow lumen just below the spider, but frequently the soil is too hard. More information can be gained by careful excavation of the burrow in daylight. An army trench shovel, a small, chisel-head, rock hammer, a large pocket knife, and pruning shears are all useful for excavating in the often hard and root-bound soil. Penultimate males, easily recognized by their swollen pedipalpal tarsi, will often molt to adulthood if kept in a cool, humid, and dark environment. Just before and during the mating season (usually during the wet fall and winter months) recently matured males may be found in their burrows prior to abandoning them. Wandering males are best collected at night by hand or with pitfall traps in dense burrow aggregations during optimum mating weather.

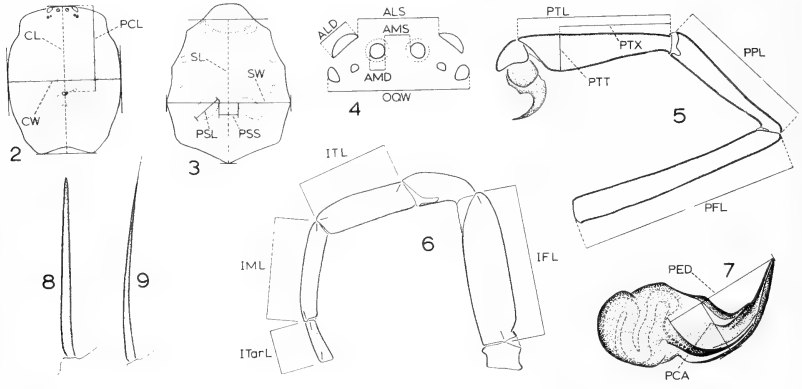
ANALYSIS OF VARIATION

I have examined the taxonomy of *Aliatypus* by means of an analysis of variation nearly identical to the analysis employed in my revisions of *Antrodiaetus* (Coyle, 1971) and *Atypoides* (Coyle, 1968). Such an analysis largely overcomes difficulties posed by the relatively simple reproductive anatomy, by the instar heterogeneity of adult female samples, and by heightened geographic variation, difficulties which appear to be common to most mygalomorph spider taxa. The material analyzed consists of 252 adult females and 78 adult males. The sample size for each species is indicated in Tables 1 and 2.

Initially, variation in a large number of qualitative and quantitative characters was briefly surveyed, and from these characters the diagnostically most promising were selected and their variation studied

in depth. Variation of the quantitative characters (measurements, meristic characters, and ratios formed from these) was analyzed with the aid of an IBM 360 Model 30 computer. A Fortran IV program directed the computer to calculate the mean and standard deviation of each character for each local population sample of each sex and for certain groupings of local samples into larger infraspecific samples or species samples. The computer then compared these samples pairwise in any desired combination, giving for each character for each comparison a value of the distinctness of the two samples. This "distance" value equals the difference between the means of the two samples divided by the sum of their standard deviations.

This variation analysis was performed with the following number of characters: 23 measurements, one meristic character, and 39 ratios for males; 20 measurements, six meristic characters, and 50 ratios for females. The measurements and meristic characters were defined so as to be clearly delimited. Their abbreviations and definitions are as follows (see Figs. 2-7):



Figures 2-7: Measurements used in *Aliatypus* revision. See text for definitions. Figures 8-9: Macrosetae types. 8: ensiform. 9: attenuate.

CL Maximum length of carapace measured as distance (along median longitudinal axis) between lines tangent to anteriormost and posteriormost edges of carapace, with lateral border of carapace in horizontal plane.

PCL Length of pars cephalica measured as distance from anterior edge of thoracic groove along median longitudinal line.

CW Maximum width of carapace along line perpendicular to median longitudinal axis.

IFL Length of femur I taken as length of straight line connecting the proximal and distal points of articulation. All leg and pedipalp segment length measurements were made in side view along retrolateral surface of appendages after removing them from spider.

ITL Length of tibia I taken as length of straight line connecting proximal and distal points of articulation.

IML Length of metatarsus I taken as length of straight line connecting proximal point of articulation with distalmost point of segment.

ITarL Length of tarsus I taken as length of straight line connecting most proximal exposed point of tarsus with distalmost point of dorsal surface.

IVFL, IVTL, IVML, IVTarL Leg IV segment lengths measured in same manner as corresponding leg I segments.

PFL Length of pedipalpal femur measured same as IFL.

PPL Length of pedipalpal patella measured as straight line distance from proximal to distal end along dorsal surface.

PTL Length of pedipalpal tibia measured same as ITL.

PTX Distance from proximal point of articulation on tibia to point where PTT line intersects PTL line.

PTT Maximum diameter, taken perpendicular to line defining PTL, of pedipalpal tibia in lateral view.

PED Straight line distance from base of embolus to tip of conductor.

PCA Maximum distance from PED line to outer edge of OCS along line perpendicular to PED line.

SL Maximum length of sternum on line parallel to median longitudinal axis. Anterior border of sternum is its pointed anterior extension lateral to labium.

SW Maximum width of sternum perpendicular to line defining SL.

PSS Minimum distance between posterior sigilla.

PSL Maximum diameter of right posterior sigillum.

OQW Maximum width of eye group (ocular quadrangle) on line perpendicular to median longitudinal axis of carapace. All eye measurements are made in dorsal view with lateral border of carapace horizontal.

ALS Minimum distance between anterior lateral eyes.

ALD Maximum diameter of left anterior lateral eye.

AMS Minimum distance between pupils (light colored saucer-shaped central area of eye) of anterior median eyes.

AMD	Transverse diameter of left anterior median eye pupil.
EGS	Number of epiandrous gland spigots. These are located just anterior to genital opening on abdomen of adult males.
CTP	Number of cheliceral teeth in prolateral macrotooth row on left chelicera.
CTR	Number of cheliceral teeth in retrolateral row of smaller macroteeth on left chelicera.
CMT	Number of cheliceral microteeth between these two rows on left chelicera.
PTSP	Number of ensiform macrosetae on prolateral surface of tarsus of female pedipalp.
PTSR	Number of ensiform macrosetae on retrolateral surface of tarsus of female pedipalp.
IMS	Number of ensiform macrosetae on metatarsus of leg I of female.

All measurements and counts were performed by myself with the same Wild M-5 stereomicroscope with 20× eyepieces and an eyepiece micrometer scale. The measurements are accurate to one micrometer unit for each of the three different powers of magnification used. One micrometer unit had the following values for the following characters: 0.0770 mm for CL; 0.0385 mm for PCL, CW, SL, SW and all leg and pedipalp segment lengths; and 0.0092 mm for PTT, PED, PCA, PSS, PSL, and all eye measurements.

A female specimen was included in a population sample only if it was reproductively active (with maturing eggs in abdomen or brood in burrow) or had a longer carapace than the smallest reproductively active female in that sample. Many first adult instar females, a few older adult instar females, and rarely a large immature female make up the portion of a sample which is not reproductively active.

MORPHOLOGICAL TERMINOLOGY

Setae. Postocular setae form a longitudinal row or longitudinal cluster along the median longitudinal axis of the pars cephalica just behind the eye group. A *macroseta* is a very large seta. Called spines by many authors, these macrosetae are attached to the exoskeleton proper by means of an obvious socket which allows for some movement. An *ensiform* macroseta is one which tapers rather abruptly at its terminal end and is therefore rigid for its entire length (Fig. 8). An *attenuate* macroseta tapers gradually and is therefore very slender distally (Fig. 9).

Palpus. The conductor of the *Aliatypus* palpus (Fig. 97) consists of an *inner conductor sclerite* (ICS) and an *outer conductor sclerite* (OCS) which lies outside and partly cradles the ICS and the *embolus.* The ICS base is forked, with the more well developed of the two branches being called the *proximal branch.*

Female genitalia. In *Aliatypus* the *bursa copulatrix,* which opens just anterior and ventral to the uterus opening in the epigastric furrow, is bilobed and weakly sclerotized. The four *seminal receptacles* (Fig. 163) are functionally paired so that the two on the right side open close to one another into the right lobe of the bursa copulatrix and the other two open together into the left lobe. Each seminal receptacle is weakly sclerotized and consists of a narrow *stalk* and a distal expanded *bulb.* The seminal receptacle is either homogeneously sclerotized or the bulb is slightly less sclerotized than the stalk. *Aliatypus* stalks are usually sinuous, frequently even highly looped or coiled. These loops and coils are not confined to a single plane and are often irregular so that the degree of looping or coiling is very difficult to quantify. It is, however, possible to make a rough quantitative comparison by counting the number of *bends* per stalk, as is done in Figure 163, when the stalk is treated as a two-dimensional structure.

Abdominal tergites. The anterior portion of the abdominal dorsum of *Aliatypus* is provided with one or more segmentally arranged, rather heavily sclerotized patches which are presumably vestigial *tergites* (Figs.45-49). These tergites are numbered from anterior to posterior, *tergite I, tergite II,* and *tergite III.* Tergite II is always present in both sexes and is always larger than tergites I or III.

METHODS OF PRESENTATION

Type specimens. The holotypes of all species described in this paper are deposited in the Museum of Comparative Zoology. All paratypes are from the type locality and are labeled as paratypes. The paratypes for each species are deposited in about equal numbers in the Museum of Comparative Zoology and the American Museum of Natural History. Quantitative character values are given for each holotype in Table 3.

Key. Whenever quantitative characters are used in the key, the known range of values is used. Proceed cautiously when these ranges are based upon very small samples. Sample size for each species is given in Tables 1 and 2.

Diagnoses. Each diagnosis lists, in the approximate order of their usefulness, those characters most useful in identifying a given species.

Proceed cautiously when using diagnoses based upon very small samples. In Tables 1 and 2 the diagnostically most useful character values are circled for each species or group of species.

Descriptions. The quantitative character values recorded in Tables 1 and 2 are an essential part of each species description. Each description is a composite of all adult specimens at hand. Only characters of at least some diagnostic value are included. Colors are described from fully sclerotized specimens dead for two months to six years and immersed in alcohol under strong fluorescent light.

Illustrations. Illustrations were carefully drawn in pencil on translucent paper over a squared grid template with the aid of a squared grid reticle in the eyepiece of the Wild M-5 stereomicroscope. The penciled drawings were then traced in ink on heavier paper. Nearly all figures of seminal receptacles are drawn from reproductively active females.

Variation discussions. For each species, variation of all 63 male quantitative characters, all 76 female quantitative characters, and a number of qualitative characters was examined, and all characters which show marked variation are discussed. The sizes of all population samples discussed can be found in the modified Dice-Leraas diagrams or in the records section.

Records. Only specimens which I have examined are listed. Within each county citation, all records from a given locality are separated from those of other localities by a dash. Collection dates are listed only for males. When a male symbol is surrounded by parentheses, it means that the specimen was collected when immature on the date given and matured later in captivity. When no male or female symbol follows a record, this means that only immatures were collected.

Taxonomy

ALIATYPUS Smith, 1908

Aliatypus Smith, 1908, Ann. Ent. Soc. Amer., 1(4): 231. Type species by monotypy *Atypoides californica* Banks, 1896, Jour. New York Ent. Soc., 4(4): 88 — Bonnet, 1955, Bibliographia Araneorum, 2:225. — Coyle, 1971, Bull. Mus. Comp. Zool., 141(6): 372.

Descriptive diagnosis. Carapace: Figs. 45-53. Thoracic groove a deep pit which varies greatly in shape (from transverse to slightly longitudinal; borders rounded or angular); may be absent or reduced to a shallow depression. A large seta on ocular prominence

between anterior median eyes. *Chelicerae:* Figs. 39-40, 45-49. Female with row of 6 to 13 macroteeth on prolateral edge; another row of 2 to 7 smaller macroteeth on retrolateral side of closed fang; and 4 to 68 microteeth between these rows. Male also with retrolateral row of cheliceral teeth. Anterior dorsal outline of chelicerae evenly rounded in both sexes. Female with rastellum. *Pedipalps:* Figs. 78-91, 96-120. Femur, patella, and tibia of male very elongate. Male tibia swollen at least ventrally near distal end. Embolus very long and slender. Outer (convex) edge of OCS folded over to cradle embolus. ICS extends to but not beyond OCS tip, and is intimately combined distally with OCS. Ridge runs most of length of ICS. *Legs:* Figs. 92-95. One to 4 (rarely more than 1) trichobothria dorsally near distal end of metatarsus IV. Male tibia and metatarsus I each with macrosetae distributed in scattered but consistent pattern ventrally over most of length. *Spinnerets:* Figs. 43-44. Three pairs (AL, PM, PL); all functional (with spigots). AL spinnerets 2-segmented with at least several spigots clustered at tip of distal segment. PM spinnerets unsegmented. PL spinnerets 3-segmented; distal segment shorter than other two together. *Genitalia:* Figs. 121-194. Bursa copulatrix bilobed and usually very weakly sclerotized. Seminal receptacles paired, each pair opening into one lobe of bursa copulatrix. Stalks weakly sclerotized and usually relatively elongate and sinuous. Bulbs as sclerotized or slightly less sclerotized than stalks. *Behavior:* Burrow entrance a trapdoor. Egg sac pendulous and occludes burrow lumen.

The following features of *Antrodiaetus* and *Atypoides* readily distinguish them from *Aliatypus:* Thoracic groove very narrow and longitudinal. No row of large cheliceral teeth on retrolateral side of closed fang. Male pedipalp, especially patella, relatively short. ICS tip distinctly separated from OCS tip. Metatarsus IV with 5 to 21 trichobothria dorsally near distal end. AL spinnerets absent or unsegmented with at most one spinneret apically. Burrow entrance a collar or turret. Egg sac attached to one side of wall and does not occlude burrow lumen.

The following features of the Mecicobothriidae readily distinguish it from *Aliatypus:* Thoracic groove very narrow and longitudinal. No single large seta between anterior median eyes. No row of large cheliceral teeth on retrolateral side of closed fang. No rastellum. Male pedipalp, especially patella, relatively short. Metatarsus IV with more than 4 trichobothria dorsally near distal end. PL spinnerets very elongate; distal segment as long or longer than two basal segments combined. Sheet web retreat without trapdoor.

Discussion. As I have said earlier in this paper and before (Coyle, 1971), *Aliatypus* may be as closely related to the Mecicobothriidae as to the other antrodiaetid genera, *Antrodiaetus* and *Atypoides.* However, it is best to retain *Aliatypus* within the family Antrodiaetidae until a careful comparative study of all atypoid mygalomorph taxa demonstrates otherwise.

As discussed earlier, *A. californicus, A. janus, A. isolatus, A. aquilonius,* and *A. gnomus* form a group of closely related species, *A. trophonius, A. erebus, A. plutonis,* and *A. torridus* form another group of closely related species, and *A. gulosus* is quite distinct from all other *Aliatypus* species. I will not formally designate species groups, however, because the placement of *A. thompsoni,* which appears to be intermediate in its relationship to the two groups of species, would be rather arbitrary.

Key to Species of *Aliatypus*

Males

1. Palpus unique (Fig. 110); sperm reservoir looped very loosely, and embolus base close to ICS base. Pedipapal tibia (Fig. 85) banana shaped and elongate; PTX/PTL = 0.37-0.45. ..... *gulosus*

   Palpus otherwise (Figs. 96-109, 111-120); sperm reservoir much more tightly coiled, and embolus base distant from ICS base. Pedipalpal tibia (Figs. 78-84, 86-91) not banana shaped; PTX/PTL = 0.64-0.82. 2

2. PSL/PSS = 1.28-2.38. CL/IML = 1.02-1.24. Tibia and metatarsus I (Fig. 93) with short ensiform macrosetae and strongly appressed background setae. Thoracic groove nearly always absent or shallow. ..... *thompsoni*

   PSL/PSS = 0.14-1.17. CL/IML = 1.37-2.07. Tibia and metatarsus I (Figs. 92, 94-95) with more elongate macrosetae and suberect or erect background setae. Thoracic groove a deep pit. 3

3. Weakly sclerotized, finger-like extension at tip of conductor (Fig. 106). PTL/PPL = 1.03-1.06 *and* CL/PSS = 4.80-5.31. ..... *aquilonius*

   No such extension at tip of conductor (Figs. 96-105, 107-120). PTL/PPL = 1.10-1.46 *or* CL/PSS = 5.50-10.34. 4

4. ICS forms at least a weak keel distally (Figs. 96-101) 5

   Conductor *either* without a keel (Figs. 102-113, 119-120), *or,* if keel present, then it is an extension of the OCS and is closer to the conductor tip (Figs. 114-118). 6

5. PFL = 3.07-3.54 mm. CL/PPL = 1.66-1.67. ICS keel weak and conductor tip quite slender (Fig. 101). ..... *gnomus*
   PFL = 4.08-6.73 mm. CL/PPL = 1.33-1.61. ICS keel stronger and conductor tip not as slender (Figs. 96-100). ..... *californicus*
6. Distal one-fourth of conductor slender and tapers evenly (Figs. 102-105, 107-109), *and* PTX/PTL = 0.73-0.82. 7
   Either the distal one-fourth of conductor at least moderately broad and keel-like and tapers suddenly to point at end (Figs. 114-118), *or* PTX/PTL = 0.64-0.68. 8
7. CL/ALS = 7.70-8.08. Known only from Arizona. ..... *isolatus*
   CL/ALS = 8.70-11.11. Known only from California. ..... *janus*
8. PTX/PTL = 0.64-0.68. PTL/PPL = 1.31-1.32. Distal half of pedipalpal tibia venter *not* much more swollen than proximal half (Fig. 91). Palpus as in Figs. 119 and 120. *torridus*
   PTX/PTL = 0.72-0.78. PTL/PPL = 1.02-1.22. Distal half of pedipalpal tibia venter much more swollen than proximal half (Figs. 87-90). Palpus as in Figs. 114-118. 9
9. CL/IFL = 1.03-1.08. ..... *plutonis*
   CL/IFL = 1.25-1.33. 10
10. CL/PCA = 6.64-6.96. CL/AMD = 21.7-22.5. CL = 2.9-3.7 mm. Palpus as in Fig. 116. ..... *trophonius*
    CL/PCA = 9.17-9.56. CL/AMD = 25.2-34.8. CL = 4.4-6.6 mm. Palpus as in Figs. 114-115. ..... *erebus*

Females

1. Seminal receptacle stalks straight and short (Figs. 151-154). ..... *gulosus*
   Seminal receptacle stalks sinuous (Figs. 121-150, 155-194). 2
2. Thoracic groove absent or only a shallow depression (Figs. 52-53). IMS/PSS = 33.3-116.6. ..... *thompsoni*
   Thoracic groove a deep pit (Figs. 47, 49). IMS/PSS = 6.1-34.7 3
3. CL/IVTL = 2.29-2.86. SW/PSL = 6.19-20.00. PSL/PSS = 0.13-0.67. 4
   CL/IVTL = 2.88-3.52. SW/PSL = 3.81-6.56. PSL/PSS = 0.55-2.00. 8
4. AMD/AMS = 1.36-1.71. Seminal receptacle stalks weakly sinuous (Figs. 149-150). ..... *gnomus*
   AMD/AMS = 0.39-1.06. Seminal receptacle stalks strongly sinuous (Figs. 121-148). 5

5. Known only from Arizona. ..... *isolatus*
   Known only from California. 6
6. IFL/IVFL = 0.96-1.02. ITarL = 0.46-0.80. ..... *aquilonius*
   IFL/IVFL = 1.02-1.13. ITarL = 0.92-1.38. 7
7. Seminal receptacle stalks about equal diameter throughout length (Figs. 121-131). ..... *californicus*
   Seminal receptacle stalks usually much thicker basally than at distal end (Figs. 132-143). ..... *janus*
8. IVFL/IVML =1.02-1.08. ..... *plutonis*
   IVFL/IVML = 1.11-1.23. 9
9. IFL = 1.84-2.84. CL/PTSR = 0.98-1.31. Seminal receptacle stalks proportionately long and with 3-5 bends; bulbs small to medium sized (Figs. 172-173). ..... *trophonius*
   IFL = 3.27-5.38. CL/PTSR = 1.39-3.03. Seminal receptacle stalks proportionately shorter, with 1-3 bends; bulbs medium sized to very large (Figs. 174-187, 192-194). 10
10. CMT = 4-11. CL/OQW = 3.43-3.99 ..... *torridus*
    CMT = 11-68. CL/OQW = 4.05-4.93. ..... *erebus*

Aliatypus californicus (Banks)

Figures 10-17, 39, 45-48, 54, 65, 78-79, 92, 96-100, 121-131. Map 2.

Atypoides californica Banks, 1896, Jour. New York Ent. Soc., 4(4): 88. Holotype a penultimate male from Black Mountain, California, 23 October, in Museum of Comparative Zoology; examined.

Aliatypus californicus: Smith, 1908, Ann. Ent. Soc. Amer., 1(4): 232. — Comstock, 1912, The Spider Book, p. 251. — Gertsch, 1949, American Spiders, p. 132. — Bonnet, 1955, Bibliographia Araneorum, 2: 225. — Coyle, 1971, Bull. Mus. Comp. Zool., 141(6): 372. — Kaston, 1972, How to Know the Spiders, p. 60.

Comments on the type locality and previous descriptions. Banks (1896) wrote only "Black Mtn., Calif." for the type locality. Other species described in the same paper were collected by the same collector (R. W. Doane) from the Palo Alto area. This implies that the type locality of *A. californicus* is Black Mountain in northwestern Santa Clara County. Smith (1908), who knew Doane well, states confidently that the type was collected on Monte Bello Ridge of this mountain. The following species description is based partly upon a male and a female collected on Montebello Road, presumably very close to the type locality.

Banks' (1896) description is based upon an immature specimen, is brief, and does not include characteristics which distinguish *A. californicus* from some other *Aliatypus* species. Smith's (1908) de-

scription is more thorough, includes illustrations, and describes a crucial diagnostic feature, the ICS keel. This shows up in Fig. 4a of Smith's Plate XV. Although Smith correctly states that the pedipalpal tibia is longer than the patella, he erred in drawing it shorter (Smith's Fig. 3, Plate XV). The specimens upon which Smith based his description were placed in the Stanford University collection but have since been lost. Having closely examined the type specimen and Smith's description, I am confident that the material upon which the following description is based is conspecific with that described by Banks and Smith.

Diagnosis. Males: The presence of a keel on the ICS together with the shape of the conductor tip (Figs. 96-100) distinguish this species from all others. Closely related *A. janus* differs from *A. californicus* in the ratio IML/ITarL (Table 1). *A. isolatus,* also closely related, is distinguished by the ratios IML/ITarL, PPL/PFL, and PTL/PPL (Table 1). Any of the other species can be separated from *A. californicus* with the appropriate ratio selected from the following: CL/IML, CL/PSL, and PTL/PPL (Table 1). *Females: A. californicus* females are difficult to distinguish from those of *A. janus* and *A. isolatus. A. californicus* seminal receptacle stalks are of about equal diameter throughout (Figs. 121-131), unlike those of *A. janus* (Figs. 132-143) and *A. isolatus* (Figs. 144-146) which are much narrower distally than at the basal end. In *A. isolatus* the postocular row of cephalic setae extends to a point one-half or more of the distance from the anterior edge of the carapace to the thoracic groove; in *A. californicus* it extends to a point less than one-half the distance to the thoracic groove. *A. aquilonius* and *A. gnomus,* both closely related to *A. californicus,* can be distinguished from the latter by their small body size (Table 2; especially ITarL). *A. aquilonius* has distinctively smaller CL/PTSR and IFL/IVFL values (Table 2) and seminal receptacles with more swollen stalk bases (Figs. 147-148) than *A. californicus* (Figs. 121-131). *A. gnomus* has a distinctively larger AMD/AMS value (Table 2) and shorter, less sinuous seminal receptacles (Figs. 149-150) than *A. californicus* (Figs. 121-131). All other species can be separated from *A. californicus* by either seminal receptacle form or appropriate ratios chosen from the following (Table 2): CL/IFL, CL/ITL, CL/IML, SW/PSL, and PSL/PSS.

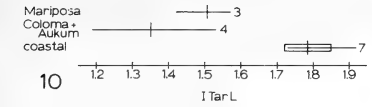
Description. See Tables 1-3.

Male: Carapace. Figs. 45-46. Thoracic groove a deep pit; usually rounded anteriorly, elongate, and tapering posteriorly; sometimes nearly circular or triangular. Postocular setae form a narrow longi-

tudinal row. *Sternum.* Fig. 54. Posterior sigilla small to medium sized and well separated. *Pedipalps.* Figs. 78-79, 96-100. Tibia strongly swollen ventrally near distal end. Embolus base well separated from ICS base. ICS ridge distally develops into thin keel which then disappears so that conductor tip is pointed. Inner (concave) edge of OCS nearly smooth to rough. *Leg I.* Fig. 92. Tibia and metatarsus with ventral, suberect, mostly attenuate macrosetae. Rest of metatarsus setae mostly long, slender, and suberect. *Abdomen.* Figs. 45-46. Tergites I and III reduced to small patches or spots at bases of macrosetae. *Coloration.* Pars thoracica light yellow to pale yellow-brown. Pars cephalica darker; light brown to medium brown; darkest along margin and median longitudinal line. Chelicerae like pars cephalica. Pedipalpal femur and patella dorsally a darker orange-brown or red-brown.

Females: Carapace. Figs. 47-48. Thoracic groove a relatively small deep pit of varying shape; usually rounded anteriorly and tapered posteriorly; sometimes circular, elongate-oval, transverse-oval, or triangular. Postocular setae form narrow row which extends back to a point ⅓ to almost ½ of distance from anterior edge of carapace to thoracic groove. *Sternum.* Fig. 65. Posterior sigilla small to medium sized and well separated. All or nearly all peripheral sternal setae slender; a few may be moderately stout. Longest setae scattered all over sternum, but more abundant anteriorly. *Chelicerae.* Figs. 39, 47-48. *Genitalia.* Figs. 121-131. Seminal receptacle stalks weakly sclerotized, nearly constant diameter throughout length, long, and with 3 to 9 bends (usually 6 to 9 bends). Bulbs relatively small to medium sized, slightly less sclerotized than stalks. *Coloration.* Pars thoracica light yellow to light grey-yellow. Pars cephalica darker; often especially dark around margin and median longitudinal line; darker parts medium brown to darker red-brown; lighter parts light yellow-brown to orange-brown. Chelicerae match darker parts of pars cephalica.

Variation. Males: The coastal population samples average considerably larger in body part dimensions than the Sierran population samples, with the sharpest discontinuity being in PED, PTT, and ITarL (Fig. 10). Somewhat discontinuous geographic variation is found in the ratios CL/PPL (Fig. 11), CL/PTX (Fig. 12), and PPL/PFL. This and weaker variation in other characters show a recurrent pattern: some phenotypic discontinuity between the rather homogeneous coastal populations on the one hand and the Sierran populations on the other; considerable discontinuity between the two Sierran populations, with the coastal populations more similar to the



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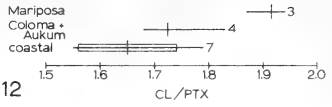

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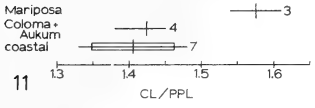

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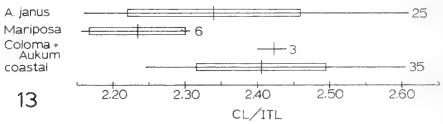

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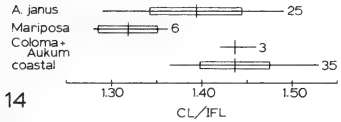

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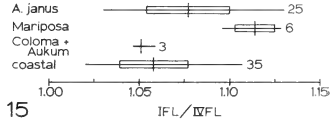

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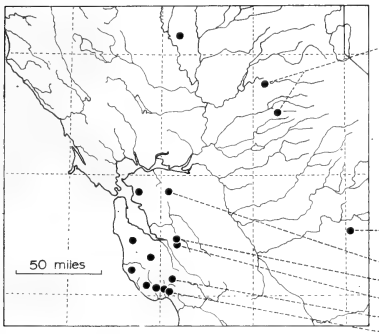

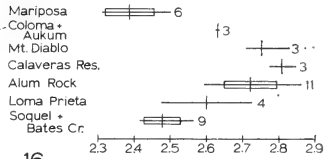

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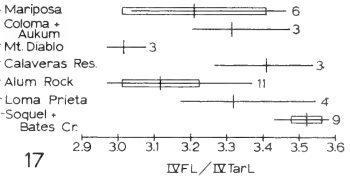

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Figures 10-17: Geographic variation of *Aliatypus californicus*. Map of sample localities and modified Dice-Leraas diagrams. (Horizontal line represents the observed range, vertical line the mean, open rectangle the standard deviation, and number to right of range line the sample size.) 10-12: males. 10: ITarL (in mm) variation. 11: CL/PPL variation. 12: CL/PTX variation. 13-17: females. 13-15: A comparison of coastal *A. californicus*, Sierran *A. californicus*, and *A. janus*. 13: CL/ITL variation. 14: CL/IFL variation. 15: IFL/IVFL variation. 16: CL/IVTL variation. 17: IVFL/IVTarL variation.

northern Sierran (Coloma-Aukum) population than to the Mariposa population.

Noteworthy geographic variation also occurs in thoracic groove shape, pedipalpal femur shape, and conductor form. Almost all coastal specimens have an elongate thoracic pit which narrows posteriorly (Fig. 45). The Coloma-Aukum specimens have roughly circular or slightly transverse pits. The Mariposa specimens have slightly elongate pits which narrow posteriorly and have a roughly triangular shape. Coastal specimens have rather strongly bowed pedipalpal femurs (Fig. 79), Mariposa pedipalpal femurs are less strongly bowed, and Coloma-Aukum ones are nearly straight (Fig. 78). Most of the Sierran specimens have less well developed ICS keels and relatively wider conductor tips (Figs. 98-100) than do coastal specimens (Figs. 96-97). However, there is considerable variation among Sierran populations, with Coloma males having a rather well developed keel and narrow conductor tip (Fig. 98), and Mariposa males having smaller keels and proportionately wider conductor tips (Figs. 99-100).

Females: There is a moderate amount of geographic variation among the coastal populations. Although some individual population samples (especially the Mt. Diablo and Soquel area samples) are quite different from another sample in a few ratios (Figs. 16-17), no population sample is distinct from the rest of the entire coastal sample in any character. The three northern Sierran (Coloma-Aukum) specimens are quite similar to the coastal populations in all characters with the exception of seminal receptacle form. Variation in the number of stalk bends in the northern Sierran receptacles (Figs. 127-129) spans the gap between the more sinuous coastal stalks (Figs. 121-125) and the less sinuous Mariposa stalks (Figs. 130-131). Northern Sierran females tend to have proportionately large receptacle bulbs (Figs. 128-129). The Mariposa sample differs rather strongly from the coastal samples in four characters (Figs. 13-15): IFL/IVFL, IVFL/IVTL, CL/IFL, and CL/ITL. It likewise differs markedly from the northern Sierran sample in these plus a fifth, CL/IVTL (Fig. 16).

In summary, male and female variation patterns indicate that there is little, if any, gene flow between coastal and Sierran populations across the unfavorable Central Valley, that there is little gene flow between the northern and more southern Sierran populations, and that the coastal population is genetically more similar to the northern Sierran populations than to the Mariposa population. I do not feel that the variation discontinuities between coastal populations and the

Coloma-Aukum population are great enough to indicate that reproductive isolation would develop if the populations were brought together. The recent discovery in the Sutter Buttes area of the Central Valley of a moderately large immature female *A. californicus* (Fig. 126) supports this conclusion by suggesting that gene flow could have occurred rather recently across the Central Valley.

The female sample from Mariposa is quite divergent from all other *A. californicus* samples. However, without an analysis of more and larger Sierran samples, I am reluctant to conclude that this Mariposa population is a different species. It is possible but unlikely that this Mariposa female sample is conspecific with *A. janus*. The computer analysis shows that this sample is more similar to *A. janus* than to the rest of the entire *A. californicus* sample. If this population is conspecific with *A. janus,* its variation patterns shown in Figures 13-15 could be the result of character displacement with the sympatric *A. californicus* population. However, the collection of three *A. californicus* males in the same location with the Mariposa females argues strongly against this possibility.

Distribution. Mountains and foothills of the San Francisco Bay region, western foothills of the Sierra Nevada Mountains, and at least one area in the Central Valley (Map 2).

Records. CALIFORNIA. COASTAL POPULATIONS: *Contra Costa Co.:* 0.5 mi. E of South Gate of Mt. Diablo St. Pk., 1300 ft., 3♀. — Orinda Village. *San Mateo Co.:* Butano State Park, ♀. — Huddart Park, ♀. *Santa Clara Co.:* Montebello Rd., 4 mi. W of junc. with Stevens Canyon Rd., 2300 ft., 10 Oct. 1971, ♂, ♀. — Mt. Loma Prieta, 9 mi. W of Morgan Hill, 1800 ft., 10 Oct. 1970, ♂, 4♀. — Marsh Rd., 0.5 mi. S of Calaveras Reservoir, 900 ft., 7 Oct. 1970, 2♂, 3♀. — Alum Rock Park, 600 ft., 11 Oct. 1970, ♂, ♀; 23 Oct. 1970, ♂, 3♀; 7♀. *Santa Cruz Co.:* 4.5 mi. N of Soquel Center, 300 ft., 12 Oct. 1971, ♂, 4♀; 2♀. — Bates Creek, 3 mi. NE of Soquel, 200 ft., 3♀. — Henry Cowell St. Pk., Redwood Loop Nature Trail, 250 ft., ♀. — 1.7 mi. W of Felton on Felton Empire Rd., 1000 ft., ♀. — 4.3 mi. W of Felton on Ice Cream Grade Rd., 1600 ft. SIERRAN POPULATIONS: *El Dorado Co.:* Omo Ranch Rd., 1.5 mi. NE of Aukum, 2200 ft., 9 Nov. 1972, ♂, 2♀. — 0.5 mi. SE of Coloma, 750 ft., 8 Nov. 1972, 3♂, ♀. *Mariposa Co.:* 0.5 mi. NW of Mariposa on rt. 49, 2000 ft., 14 Oct. 1969, (♂), ♀; 8 Oct. 1971, 2♂, 3♀; 2♀. CENTRAL VALLEY POPULATION: *Sutter Co.:* Moore Canyon of Sutter Buttes, 4.5 mi. NW of Sutter, 200 ft.

Aliatypus janus new species

Figures 18-24, 55, 66, 83-84, 102-105, 132-143. Map 2.

Type specimens and etymology. Holotype male from 5 mi. south of Hume Lake, Fresno Co., California, 16 October 1973 (W. R. Icenogle). One male and three female paratypes. Janus was the Latin god of gates and doors.

Diagnosis. Males: A. janus is very similar to *A. isolatus;* CL/ALS (Table 1) is useful in separating these two allopatric species. *A. janus* is distinct from closely related *A. californicus* in the absence of an ICS keel (Figs. 102-105) and in IML/ITarL (Table 1). *A. janus* is distinct from *A. aquilonius* in palpus tip form (Figs. 102-105), SW/PSS, CL/PSS, and CL/ALS (Table 1). *A. janus* differs from *A. gnomus* in CL/ALS, CL/AMD, and body size (Table 1). Sympatric *A. erebus* differs from *A. janus* in CL/PTT, PSL/PSS, CL/IFL (Table 1), and palpus form (Figs. 102-105). *A thompsoni,* also sympatric with *A. janus,* is distinct in PSL/PSS, CL/IML (Table 1), thoracic groove form, and leg I setation. Other species can be separated from *A. janus* with an appropriate ratio from the following (Table 1): CL/ALS, PTX/PTL, and PTT/PTL. *Females:* The only really helpful character to use in separating *A. janus* from closely related *A. isolatus* is SL/SW (Table 2). Only seminal receptacle form appears useful in separating *A. janus* from closely related *A. californicus* (See *A. californicus* diagnosis). *A. janus* has a larger IFL/IVFL, longer ITarL, and more IMS (Table 2) than does *A. aquilonius. A. janus* is distinct from *A. gnomus* in AMD/AMS, IFL/IVFL, body size (Table 2), and seminal receptacle form (Figs. 132-143). *A. janus* is distinct from sympatric *A. erebus* in seminal receptacle form (Figs. 132-143), CL/PSL, SW/PSL, and IFL/IVFL (Table 2). *A. janus* is distinct from sympatric *A. thompsoni* in thoracic groove form, seminal receptacle form (Figs. 132-143), CL/PSS, and PSL/PSS (Table 2). The remaining *Aliatypus* species can be separated from *A. janus* by either CL/IFL or IFL/IVFL (Table 2), and by seminal receptacle form (Figs. 132-143).

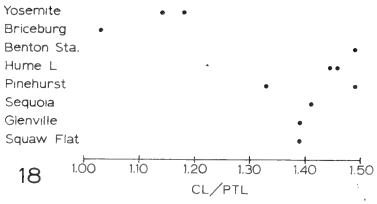
Description. See Tables 1-3.

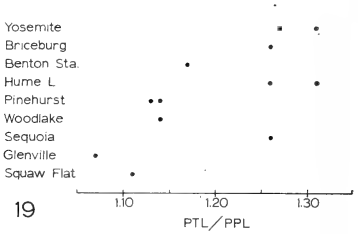
Males: Carapace. Thoracic groove a deep pit; usually roughly triangular or T-shaped. Postocular setae form moderately long narrow row. *Sternum.* Fig. 55. Posterior sigilla small to medium sized and well separated. *Pedipalps.* Figs. 83-84, 102-105. Tibia markedly swollen ventrally near distal end. Embolus base distant from ICS

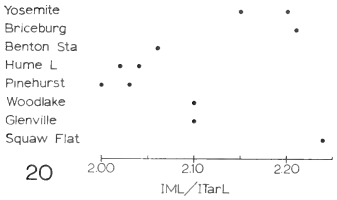
base. Conductor tapers evenly to narrow tip which is sharp or angularly truncate; tip may be bent or straight. Inner (concave) edge of OCS smooth to somewhat rough. *Leg. I.* A few to all ventral macrosetae on tibia and metatarsus are ensiform; background setae long, slender, not appressed, and very densely distributed. *Abdomen.* Tergites I and III reduced to small patches or spots at bases of macrosetae. *Coloration.* Pars thoracica pale yellow to light brown. Pars cephalica markedly darker; medium to dark red-brown or chestnut. Chelicerae usually slightly darker red-brown than pars cephalica. Dorsal surface of pedipalpal patella and tibia same as chelicerae or darker.

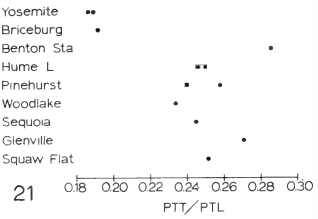
Females: Carapace. Thoracic groove a deep pit; usually roughly triangular or T-shaped; rarely a transverse furrow, transversely oval, or circular. Postocular setae form a very narrow longitudinal row. *Sternum.* Fig. 66. Posterior sigilla medium sized and well separated. Great majority of peripheral sternal setae slender; usually a few to many stout ones on anterior-lateral margins. Longest setae scattered over most of sternum, but slightly more abundant anteriorly. *Genitalia.* Figs. 132-143. Stalks of seminal receptacles very weakly to moderately heavily sclerotized; almost always much thicker at base than at distal end; weakly to strongly sinuous (3-9 bends). Bulbs small to medium sized; less sclerotized than stalks. *Coloration.* Pars thoracica pale yellow to rather dark yellow-gray. Pars cephalica slightly to much darker; pale brown to chestnut; median longitudinal band and posterior border darker than rest. Chelicerae orange-brown, red-brown, or chestnut; slightly darker than dark part of pars cephalica.

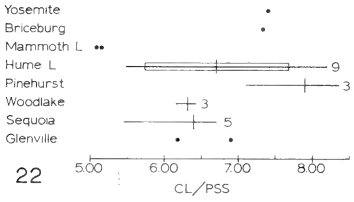
Variation. Males: Although the male population samples are very small, they should provide at least an indication of the geographic variation patterns within this species. The strongest geographic variation occurs in pedipalpal tibia shape and conductor tip form. As Figures 18, 21, 83, and 84 indicate, the Yosemite and Briceburg specimens have markedly more elongate and slender pedipalpal tibiae than do the other samples. However, because of a relatively short pedipalpal patella, the Hume Lake and Sequoia specimens exhibit a PTL/PPL ratio similar to the Yosemite and Briceburg specimens and distinct from the other samples (Fig. 19). Although conductor tip shape varies considerably, the variation is rather continuous and clinal (Figs. 102-105). The Yosemite conductor tips (Fig. 103) are rounded in ventral view and strongly bent dorsad. The Briceburg conductor tip is very similar except that it is not as strongly bent dorsad. The Benton Station conductor tip is like the Yosemite tips.

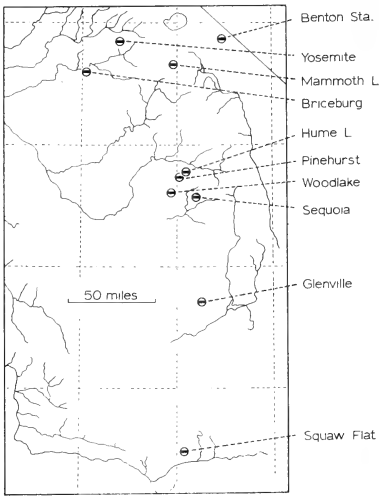


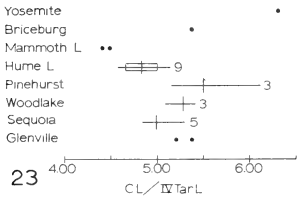


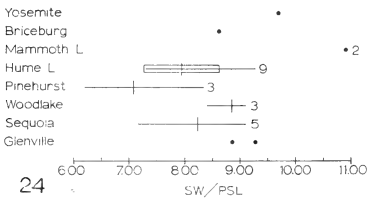












Figures 18-24: Geographic variation of *Aliatypus janus*. Modified Dice-Leraas diagrams and map of sample localities. 18-21: males. 18: CL/PTL variation. 19: PTL/PPL variation. 20: IML/ITarL variation. 21: PTT/PTL variation. 22-24: females. 22: CL/PSS variation. 23: CL/IVTarL variation. 24: SW/PSL variation.

The Hume Lake conductor tips (Fig. 102) are blunt or slightly angularly truncate, and bend dorsad almost as strongly as the Yosemite conductor tips. The Pinehurst conductor tips (Fig. 104) are slightly broader and thicker, are angularly truncate, and bend only very slightly dorsad. The Woodlake, Glenville (Fig. 105), and Squaw Flat conductor tips are similar to those at Pinehurst, but are more angularly truncate and completely unbent.

Rather strong variation occurs in the ratio IML/ITarL (Fig. 20), with Yosemite and Briceburg specimens distinct from Hume Lake and Pinehurst specimens. Tibia and metatarsus I setation varies geographically with Yosemite, Briceburg, Benton Station and Hume Lake specimens having 10 to 50 percent of the ventral macrosetae ensiform and relatively long densely distributed background setae. All other specimens have 70 to 100 percent of the ventral macrosetae ensiform, and shorter, less erect, less densely distributed background setae. The Yosemite and Briceburg specimens differ from the rest in that the pars thoracica is not markedly lighter than the pars cephalica. The Yosemite and Benton Station specimens differ from the rest in that the postocular setae extend back to a point at one-half or more of the distance from the anterior edge of the cephalothorax to the thoracic groove.

Females: The female population samples also show a considerable amount of geographic variation, which is not surprising for such a widespread species. The chief variation pattern is that most samples (Hume Lake, Pinehurst, Woodlake, Sequoia, and Glenville) are quite similar, but that the northern samples (Yosemite, Briceburg, and Mammoth Lakes) do not form as homogeneous a grouping and each differs almost distinctively from most other samples in a few characters. The very small sample sizes limit the strength of any conclusions.

Discontinuous geographic variation in quantitative characters involves those ratios incorporating PSS and PSL (Figs. 22 and 24). In these ratios the Mammoth Lakes population, with its smaller, more widely spaced posterior sigilla, is quite divergent. CL/IVTarL (Fig. 23) exhibits rather strong geographic variation with the Yosemite specimen very divergent. Other quantitative characters exhibit less geographic variation.

Variation in seminal receptacle form is illustrated by Figures 132-143. All samples except those from the Yosemite-Briceburg area have very similar seminal receptacles. In both the Yosemite and Briceburg specimens, the stalk base is not much thicker than the distal end, a condition similar to that of *A. californicus*. Additional

noteworthy variation among female samples is as follows: the Mammoth Lakes, Pinehurst, Woodlake, and Glenville specimens are lighter colored than most specimens from other localities; the Woodlake and Glenville specimens have zero to two stout peripheral sternal setae (nearly all other specimens have many more) and fewer postocular setae than nearly all other specimens.

Variation in both sexes indicates, not surprisingly, that gene flow is restricted in portions of this species' geographic range. Gene flow between the more northern populations (Yosemite, Briceburg, Benton Station, and Mammoth Lakes) and those to the south may be especially restricted. Possible competition or hybridization with *A. californicus* in the area of sympatry around Mariposa may have an important effect upon the genetics of these northern populations. The Yosemite and Briceburg specimens are especially divergent and may eventually prove to represent a distinct species. Obviously, more and larger samples must be collected in order to obtain an accurate picture of geographic variation and of factors affecting gene flow within this species.

Distribution. Central and southern Sierra Nevada Mountains and part of the Coast Range Mountains north of Los Angeles (Map 2).

Records. CALIFORNIA. *Fresno Co.:* Loop road 5 mi. S of Hume Lake, 6000 ft., 16 Oct. 1973, 2♂, 9♀. — Hwy. 245, 1 mi. E of Pinehurst, 4300 ft., 18 Oct. 1973, 2♂, 3♀. *Kern Co.:* Glenville, 15 Nov. 1969, ♂. — 10 mi. SW of Glenville, 2♀. *Madera Co.:* 7 mi. W of Mammoth Lakes, 8700 ft. 2♀. *Mariposa Co.:* near Briceburg, 1300 ft., ♂. — 4 mi. N of Briceburg on Hwy. 140, 1300 ft., ♀. — Yosemite Nat'l Pk., 3.4 mi. E of Yosemite Cr. bridge on Hwy. 120, about 8000 ft., 10 Aug. 1972, 2♂. — Yosemite Nat'l Pk., 20 mi. E of Crane Flat on Hwy. 120, about 8000 ft., ♀. *Mono Co.:* Benton Station, 26 Oct. 1941, ♂. *Tulare Co.:* Sequoia Nat'l Pk., Congress trail near General Sherman Tree, 6800 ft., 13-14 Aug. 1972, ♂, 5♀. — 14 mi. N of Woodlake on Hwy. 69, 1200 ft., 10 Nov. 1972, ♂, 3♀. *Ventura Co.:* 5.5 mi. S of Squaw Flat, 29 Nov. 1970, ♂.

Aliatypus isolatus new species

Figures 56, 67, 80, 107-109, 144-146. Map 3.

Type specimens and etymology. Holotype male from Cave Springs Campground, about 9 mi. north of Sedona in Oak Creek Canyon, Coconino Co., Arizona, 19 August 1972 (F. A. Coyle). One male and four female paratypes. The specific name is a Latin adjective meaning isolated.

Diagnosis. The geographic range of this species (Map 3) is well separated from those of all other *Aliatypus* species. *Males:* Because of its proportionately long metatarsus I, short tarsus I, and short pedipalpal patella, *A. isolatus* is best distinguished from most of its congeners by the ratios IML/ITarL, PPL/PFL, and PTL/PPL (Table 1). The palpus structure (Figs. 107-109) of *A. isolatus* is distinctly different from that of most species. CL/ALS (Table 1) is the best character for distinguishing *A. isolatus* from closely related *A. janus. Females: A. isolatus* is extremely similar to *A. janus* and *A. californicus;* refer to diagnoses of these species. *A. isolatus* differs from similar *A. aquilonius* in having a transverse thoracic pit rather than a rounded or elongate one, and in its larger body size (especially longer tarsi; Table 2). *A. isolatus* can be separated from *A. gnomus* by seminal receptacle form (Figs. 144-146), AMD/AMS and CL/AMD (Table 2), and body size (Table 2). CL/IVTL, CL/IFL, and PSL/PSS (Table 2) clearly distinguish *A. isolatus* from all other species.

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep transverse pit or groove. Postocular setae form a relatively long narrow row. *Sternum.* Fig. 56. Posterior sigilla small and far apart. *Pedipalp.* Figs. 80, 107-109. Tibia swollen ventrally near distal end. Embolus base distant from ICS base. Conductor tapers rather evenly to narrow, sharp, angularly truncate tip which is bent. Inner (concave) edge of OCS smooth. *Leg I.* Tibia and metatarsus with all or nearly all ventral macrosetae attenuate; background setae elongate, slender, densely distributed, and not appressed. *Abdomen.* Tergite I small. Tergite III absent. *Coloration.* Pars cephalica and chelicerae light brown to dark brown; much darker than light grey-yellow pars thoracica. Pedipalps darker than pars cephalica; medium orange-brown to dark red-brown.

Females: Carapace. Thoracic groove a deep transverse pit or groove. Postocular setae row extends to point at least one-half of distance from anterior edge of carapace to thoracic groove. *Sternum.* Fig. 67. Posterior sigilla small and far apart. Peripheral setae slender. Longest setae scattered all over sternum. *Genitalia.* Figs. 144-146. Seminal receptacles weakly sclerotized. Base of stalk relatively thick and nearly straight. Stalk becomes much narrower distally; long; 4-7 bends; often very irregularly looped. Bulbs small. *Coloration.* Pars thoracica pale yellow to pale yellow-brown. Pars cephalica darker; light yellow-brown to medium brown. Chelicerae slightly darker than pars cephalica.

Variation. Males: A comparison of the two small samples of two males each indicates rather strong geographic variation. The Oak Creek Canyon sample has a markedly larger body size (CL = 4.8 mm, 4.9 mm), a proportionately longer pedipalpal patella (CL/PPL = 1.53, 1.64), and darker coloration than the Santa Catalina Mountain sample (CL = 3.5 mm, 3.8 mm; CL/PPL = 1.75, 1.77). The conductor tip is proportionately a bit narrower and is bent more strongly (Figs. 107-109) in the Oak Creek Canyon males. *Females:* No marked geographic variation occurs in any of the ratio characters. The Oak Creek Canyon sample averages larger in body size, but the ranges of the two samples overlap. Seminal receptacle stalks are more irregularly sinuous in the Santa Catalina Mountain sample than in the Oak Creek Canyon sample (Figs. 144-146). The two samples show broadly overlapping color variation.

Distribution. Arizona (Map 3).

Records. Arizona. *Coconino Co.:* 0.2 mi. S of Manzanita Campgrd. in Oak Creek Canyon about 6 mi. N of Sedona, 4400 ft., ♀. — Cave Springs Campgrd. in Oak Creek Canyon about 9 mi. N of Sedona, 4900 ft., 19 Aug. 1972, 2 ♂, 4 ♀. *Pima Co.:* Molino Basin Campgrd. in Santa Catalina Mtns., 4500 ft. — 1.5 mi. below Bear Cr. Picnic Area along Hwy. to Mt. Lemon, 5400 ft., 27 March 1970, 2 (♂), 5 ♀. — Bear Cr. Picnic Area in Santa Catalina Mtns., 5800 ft. — General Hitchcock Picnic Area in Santa Catalina Mtns., 6000 ft.

Aliatypus aquilonius new species

Figures 57, 68, 81, 106, 147-148. Map 2.

Type specimens and etymology. Holotype male from Grizzly Creek Redwoods State Park, Humboldt Co., California, 8 August 1972 (F. A. Coyle). One male and 14 female paratypes. The specific name is a Latin adjective meaning northern.

Diagnosis. Males: The weakly sclerotized, finger-like extension at the tip of the palpus (Fig. 106) is distinctive. The pedipalpal patella is proportionately long (Fig. 81), so that appropriate ratios from among the following distinguish *A. aquilonius* from any other species (Table 1): PTL/PPL, PPL/PFL, CL/PPL, CL/PSS, SW/PSS. *A. aquilonius* males are markedly smaller than those of coastal *A. californicus* and some other species (Table 1). *Females:* The following characters best distinguish *A. aquilonius* from similar species: smaller AMD/AMS (Table 2) and more strongly coiled seminal receptacle stalks (Figs. 147-148) than in

A. gnomus; smaller CL/PTSR and IFL/IVFL (Table 2) than in *A. californicus;* smaller IFL/IVFL and fewer IMS (Table 2) than in *A. janus;* fewer IMS and smaller CL/ITL (Table 2) than in *A. isolatus.* Because of its small widely spaced posterior sigilla (Fig. 68) and proportionately long tibia IV, *A. aquilonius* is easily separated from the rest of the species by the following characters (Table 2): CL/IVTL, CL/PSS, CL/PSL, SW/PSS, SW/PSL, and PSL/PSS.

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep longitudinal groove or a deep rounded pit. Postocular setae form a relatively short and narrow longitudinal band. *Sternum.* Fig. 57. Posterior sigilla faint, small, and far apart. *Pedipalp.* Figs. 81, 106. Distal half of tibia ventrally moderately swollen. Embolus base distant from ICS base. Palpus tipped with weakly sclerotized finger-like extension. Inner (concave) edge of OCS smooth. *Leg I.* Tibia and metatarsus with most of ventral macrosetae attenuate; background setae long, slender, erect, and rather sparsely distributed. *Abdomen.* Tergites I and III reduced to small patches or spots at bases of macrosetae. *Coloration.* Cephalothorax and chelicerae nearly homogeneous light yellow-brown. Pedipalps slightly darker.

Females: Carapace. Thoracic groove a deep pit; circular, irregular, or longitudinal. Postocular setae few; form a moderately long, roughly single row. *Sternum.* Fig. 68. Posterior sigilla small and far apart. Peripheral setae slender. Longest setae absent from large central area. *Genitalia.* Figs. 147-148. Seminal receptacles very weakly sclerotized. Base of stalk relatively thick, elongate, and nearly straight. Stalk long, becomes much narrower distally, 3-6 bends. Bulbs very small. *Coloration.* Cephalothorax homogeneous light yellow-brown. Chelicerae darker light brown to medium brown.

Variation. There is very little variation among the four males. *Females:* The Grizzly Creek sample (n = 12) has a markedly larger mean body size (CL = 4.60 ± .74 mm; range = 3.4 mm-5.8 mm) than the Redway sample (n = 14) (CL = 3.40 ± .41 mm; range = 2.8 mm-4.1 mm). Generally, the larger the specimen the more heavily sclerotized and elongate the posterior sigilla; the posterior sigilla are round in the smallest specimens and twice as long as wide in the largest specimens. There is continuous variation in the degree of coiling of seminal receptacles; all specimens fall between, or are similar to, the conditions illustrated by Figures 147 and 148.

Distribution. Humboldt Co. in northwestern California (Map 2).

Records. CALIFORNIA. *Humboldt Co.:* Grizzly Creek Redwoods St. Pk., 400 ft., 8 Aug. 1972, 2(♂), 12♀. — 1.4 mi. W of Redway on road to Briceland, 400 ft., 7 Aug. 1972, (♂), 14♀. —2 mi. W of Briceland, 400 ft., 15 Sept. 1971, ♂, ♀.

Aliatypus gnomus new species

Figures 49, 58, 69, 82, 101, 149-150. Map 2.

Type specimens and etymology. Holotype male from Henry Cowell Redwoods State Park, Santa Cruz Co., California, 3 August 1972 (F. A. Coyle). One male and four female paratypes. The specific name is a Latin noun meaning dwarf.

Diagnosis. Males: At least one of the following ratios (Table 1) will separate this species from any one of the other species: CL/PPL, CL/PSL, PSL/PSS, and PTL/PPL. The palpus, with an ICS keel and a slender conductor tip (Fig. 101), is quite distinct from that of all species. The ICS keel is narrower and the conductor tip more slender than in closely related *A. californicus.* These palpus features, CL/PPL, CL/PSL, and body size (Table 1) are the best characters for separating *A. gnomus* from *A. californicus.* In all of these characters, *A. gnomus* is more distinct from coastal *A. californicus* populations than from the Sierran *A. californicus* populations. *Females: A. gnomus* has distinctively large, close set AME's, so that one ratio, AMD/AMS (Table 2), clearly separates this species from all other species. Also, the weakly sinuous seminal receptacles (Figs. 149-150) are distinctive. *A. gnomus* is distinctively smaller (Table 2) than most other species.

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep rounded pit. Postocular setae form rather short narrow row which is broadest anteriorly. *Sternum.* Fig. 58. Posterior sigilla small and far apart. *Pedipalp.* Figs. 82, 101. Distal half of tibia ventrally swollen. Embolus base distant from ICS base. ICS with a thin narrow keel distally. Conductor tip slender and tapers evenly to fine point. Inner (concave) edge of OCS smooth. *Leg I.* Tibia and metatarsus with most of ventral macrosetae attenuate; background setae long, slender, moderately densely distributed and more or less appressed on tibia but suberect on metatarsus. *Abdomen.* Tergites I, II, and III all well developed; II largest. *Coloration.* Pars cephalica and chelicerae pale brown. Pars thoracica pale yellow. Pedipalps darker than pars cephalica.

Females: Carapace. Fig. 49. Thoracic groove a deep circular or longitudinally oval pit. Three or four large postocular setae form single, moderately long, row; sometimes additional tiny setae. AME's relatively large and separated by less than diameter. *Sternum.* Fig. 69. Posterior sigilla small and far apart. Peripheral setae slender. Longest setae less common centrally than toward the periphery. *Genitalia.* Figs. 149-150. Seminal receptacle stalks extremely weakly sclerotized, weakly sinuous (1-4 weak bends), and same diameter throughout length. Bulbs almost transparent and proportionately small to medium sized. *Coloration.* Pars thoracica pale yellow. Pars cephalica and chelicerae a darker pale brown.

Distribution. Known only from the type locality (Map 2).

Record. CALIFORNIA. *Santa Cruz Co.:* Henry Cowell Redwood St. Pk., along Hwy. 9, 3.3 mi. S of Felton center, 400 ft., 3 Aug. 1972, 2(♂), 4♀.

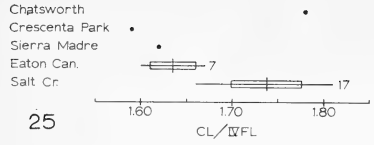
Aliatypus gulosus new species

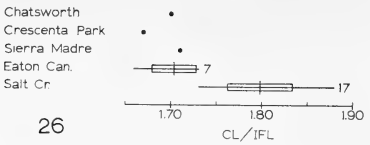
Figures 25-26, 59, 70, 85, 110, 151-154. Map 2.

Type specimens and etymology. Holotype male from Salt Creek, 1.5 miles north of Dana Point, Orange Co., California, 6 December 1968 (W. R. Icenogle). Three males and 17 female paratypes. The species name is a Latin adjective meaning gluttonous.

Diagnosis. Males: The palpus (Fig. 110) of *A. gulosus* is distinctively different from that of all other species. The very loosely looped sperm reservoir, the closeness of the embolus base to the ICS base, the jagged, serrate inner (concave) edge of the OCS, and the evenly tapered conductor tip are some of the more distinctive palpus features. The distinctive, long banana shape of the pedipalpal tibia (Fig. 85) is expressed quantitatively by the excellent diagnostic ratios (Table 1) PTX/PTL and PTL/PPL. *Females:* The seminal receptacles (Figs. 151-154) of *A. gulosus* are distinctively different from those of all other species. The stalks are short and straight and the bulbs are relatively large. The appropriate ratio selected from among the following will clearly distinguish *A. gulosus* from any other species (Table 2): CL/IFL, CL/IML, CL/PSS, SW/PSS, SW/PSL, PSL/PSS, and IMS/PSS. Any of the last five ratios distinguish *A. gulosus,* with its small, widely spaced posterior sigilla, from the other southern California species (*A. thompsoni, A. plutonis,* and *A. torridus*).

Description. See Tables 1-3.





Figures 25-26: Geographic variation of *Aliatypus gulosus* females. Modified Dice-Leraas diagrams. 25: CL/IVFL variation. 26: CL/IFL variation.

Males: Carapace. Thoracic groove a deep, roughly circular pit. Postocular setae form a roughly triangular grouping. *Sternum.* Fig. 59. Posterior sigilla small and well separated. *Pedipalps.* Figs. 85, 110. Tibia banana shaped. Sperm reservoir large and loosely looped. Embolus base very close to ICS base. Distal half of conductor tapers evenly to tip. Inner (concave) edge of OCS with minute jagged serrations. *Leg. I.* Very similar to *A. plutonis* leg I in proportions and setation. Most ventral macrosetae on tibia and metatarsus are ensiform. *Abdomen.* Tergites I, II, and III all well developed; II largest and I smallest; sometimes II and III are fused together or nearly so. *Coloration.* Carapace light yellow-brown to medium red-brown; margins of pars cephalica often slightly darker. Chelicerae like lightest parts of carapace or slightly darker. Pedipalps dorsally like lightest parts of carapace or lighter.

Females: Carapace. Thoracic groove a deep transverse pit; slightly to much wider than long. Postocular setae form a roughly double row. *Sternum.* Fig. 70. Posterior sigilla rather small and far apart. Usually, all or most peripheral sternal setae slender; stout setae most likely found near anterior-lateral margins of sternum. Longest setae scattered rather evenly over sternum. *Genitalia.* Figs. 151-154. Seminal receptacles very weakly sclerotized. Stalks short and straight. Bulbs relatively large. *Coloration.* Pars thoracica pale yellow to medium brown. Pars cephalica centrally about same color; darker (light brown to chestnut brown) around margin. Chelicerae like darker portion of pars cephalica.

Variation. While the total male sample (one male from Eaton Canyon and five from Salt Creek) is remarkably homogeneous in all characters, the female samples exhibit patterns of geographic variation which indicate some limitation to gene flow between the Salt Creek and the Los Angeles area populations. *Females:* Three characters exhibit marked geographic variation. The Salt Creek and Eaton Canyon samples differ somewhat markedly in two ratios, CL/IFL and CL/IVFL (Figs. 25-26). Also, Salt Creek specimens possess

fewer stout peripheral sternal setae than most Los Angeles area specimens; a few of the latter possess many stout setae scattered along the entire sternal margin. The Chatsworth specimen is markedly variant. All its peripheral sternal setae are stout, the very long sternal setae are almost completely limited to the anterior half of the sternum, the sternum is exceptionally wide (SL/SW = 1.02), and femur I is longer than femur IV (IFL/IVFL = 1.05). Some minor and non-geographic variation occurs in the relative positions of the seminal receptacles (Figs. 151-154).

Distribution. The Los Angeles Basin of southern California (Map 2).

Records. CALIFORNIA. *Los Angeles Co.:* Eaton Canyon Park, 3 Jan. 1965, ♂; 7♀. — Sierra Madre, Bailey Canyon, ♀. — Crescenta Valley Park, ♀. — Chatsworth, ♀. *Orange Co.:* Salt Creek, 1.5 mi. N of Dana Point, 60 ft., 6 Dec. 1968, 2♂, 4♀; 5 Sept. 1969, ♂; 12 Nov. 1969, ♂; 13♀.

Aliatypus thompsoni new species

Figures 27-33, 40-44, 50-53, 60, 71-73, 86, 93, 111-113, 155-171. Map 4.

Type specimens and etymology. Holotype male from Chatsworth, Los Angeles Co., California, 25 November 1967 (M. E. Thompson). Three male and 15 female paratypes. This species is named after Mel Thompson, who has collected most of the male specimens studied.

Diagnosis. Males: A. thompsoni is distinct from all other species in two ratio characters (Table 1), PSL/PSS and CL/IML. The posterior sigilla are large, faint, and closely spaced (Fig. 60) and metatarsus I is relatively long (Fig. 93). The relatively short ventral macrosetae, all of which are ensiform, and the appressed background setae of tibia and metatarsus I (Fig. 93) are also distinctive. The thoracic groove is nearly always absent or shallow (Figs. 50-51). *Females:* Unlike all other species, *A. thompsoni* females either have no thoracic groove or only a shallow vestige (Figs. 52-53). The small PSS (Table 2; Figs. 71-73) distinguishes this species from all others except *A. trophonius.* The large numbers of PTSR and IMS (Table 2) distinguish this species from many others. An appropriate ratio from among the following will distinguish *A. thompsoni* from any other species: CL/PSS, SW/PSS, and IMS/PSS (Table 2). *A. thompsoni* seminal receptacles (Figs. 155-171), with their long, many-looped, non-tapered stalks and relatively small to medium sized bulbs, are diagnostically useful.

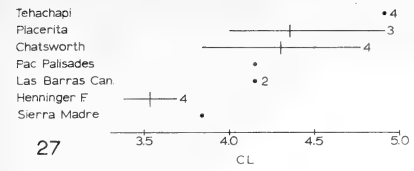
Description. See Tables 1-3.

Males: Carapace. Figs. 50-51. Thoracic groove absent, a slight double longitudinal depression, or a shallow double longitudinal pit. Postocular setae form a short narrow longitudinal row. *Sternum.* Fig. 60. Posterior sigilla faint, large, and close to one another. *Pedipalps.* Figs. 86, 111-113. Tibia strongly swollen ventrally near distal end. Embolus base distant from ICS base. Conductor tip shaped like knife blade tip. Inner (concave) edge of OCS smooth to moderately rough. *Leg I.* Fig. 93. Tibia and metatarsus with ventral, erect to suberect, relatively short, ensiform macrosetae; nearly all rest of setae appressed. *Abdomen.* Tergites I and III much smaller than tergite II; usually reduced to small patches or spots at bases of macrosetae. *Coloration.* Pars thoracica pale yellow to pale yellow-brown. Pars cephalica darker; pale brown to medium brown. Chelicerae dorsally similar to or slightly darker than pars cephalica. Pedipalps dorsally vary from pars thoracica color to cheliceral color; sometimes with orange or red tint.

Females: Carapace. Figs. 52-53. Thoracic groove absent or vestigial; if latter, it is usually a shallow depression or rarely a shallow rounded pit. 2-5 postocular setae form a very narrow longitudinal row. *Sternum.* Figs. 71-73. Posterior sigilla faint, often irregularly shaped, large, and very close together. Peripheral sternal setae all slender; sometimes a few to many anterior-lateral ones stout. Longest setae scattered over most of sternum. *Chelicerae.* Fig. 40. *Genitalia.* Figs. 155-171. Seminal receptacles extremely weakly sclerotized. Stalks very long, nearly same diameter throughout length and strongly looped (4-11 bends), sometimes irregularly. Bulbs small to medium sized. *Coloration.* Pars thoracica pale yellow to yellow. Pars cephalica darker (at least around margins and median longitudinal line); light yellow to light brown. Chelicerae darker than pars cephalica; light brown or light orange-brown to medium red-brown.

Variation. Males: Several male characters show strong geographic variation. Two variation patterns are common: often the Sierra Madre and Henninger Flats samples are similar to one another and divergent from the rest; sometimes the Tehachapi Mountain sample is divergent.

The Henninger Flats males are smaller than any others and the Tehachapi Mountain sample exhibits the largest body size average, but body size values in the other samples fill the gap between these two extremes (Fig. 27). The sternum is markedly broader (Fig. 30) and the pars cephalica is distinctly more elongate (Figs. 28, 50-51) in the Sierra Madre and Henninger Flats samples than in all others.



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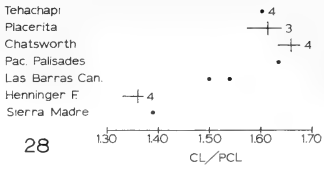

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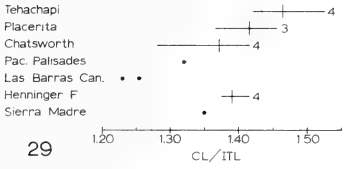

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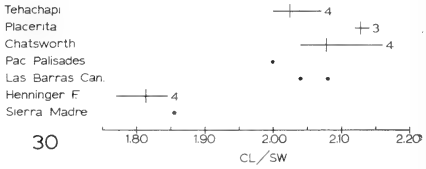

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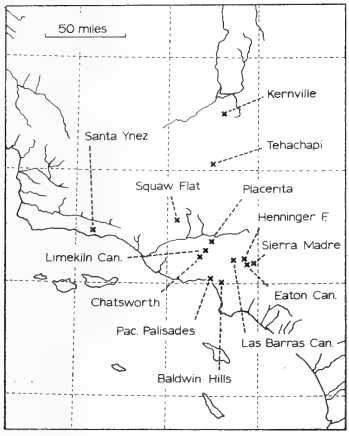

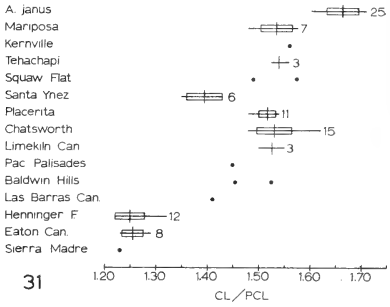

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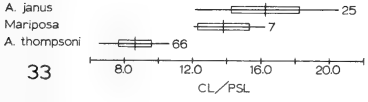

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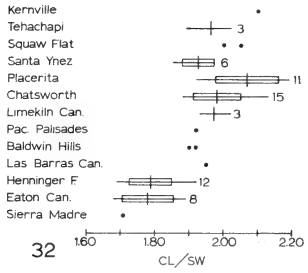

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Figures 27-32: Geographic variation of *Aliatypus thompsoni*. Modified Dice-Leraas diagrams and map of sample localities. 27-30: males. 27: CL (in mm) variation. 28: CL/PCL variation. 29: CL/ITL variation. 30: CL/SW variation. 31-32: females. 31: CL/PCL variation compared with that of *A. janus* and the enigatic Mariposa population. 32: CL/SW variation. Figure 33: Modified Dice-Leraas diagram showing CL/PSL variation of females of *Aliatypus thompsoni, A. janus,* and the enigmatic Mariposa population.

Thoracic groove form is correlated with pars cephalica shape. Those specimens (Sierra Madre and Henninger Flats) with an exceptionally elongate pars cephalica lack any vestige of a thoracic groove (Fig. 51). Specimens with a more normal pars cephalica possess at least a vestigial thoracic groove in the form of a shallow depression (Fig. 50). Tehachapi Mountain specimens have slightly to markedly deeper thoracic grooves than other specimens.

Tehachapi Mountain males have two or three trichobothria dorsally near the distal end of metatarsus IV. All other *A. thompsoni* males as well as all other *Aliatypus* males have only one trichobothrium in that position. Variation in palpus conductor tip form is illustrated by Figures 111 to 113. The Tehachapi Mountain conductor tips (Fig. 111) are slightly but consistently different from those in all other samples. Tehachapi Mountain males tend to have a darker pars cephalica and chelicerae, and redder pedipalps than do other specimens. The Las Barras Canyon specimens have noticeably more elongate legs (Fig. 29) than most others.

Females: A few female characters exhibit strong geographic variation. These are characters which also vary strongly in the male sample, and the geographic patterns of these variations are like those in the male sample.

The pars cephalica is markedly more elongate in the Sierra Madre, Eaton Canyon, and Henninger Flats samples than in all other samples (Figs. 31, 52-53). These same three southeastern samples have on the average a considerably broader sternum than most other samples (Figs. 32, 71-73). The thoracic groove is completely absent in these three samples with an elongate pars cephalica (Fig. 53), and is only a faint depression (slightly more heavily sclerotized than its immediate surroundings) (Fig. 52) in all other samples except the Tehachapi Mountain and Kernville samples. These latter specimens have a slightly deeper depression or a shallow pit.

The Tehachapi Mountain and Kernville specimens have two to four trichobothria dorsally near the distal end of metatarsus IV. All other females of *A. thompsoni* and all other *Aliatypus* species have only one such trichobothrium. Variation in seminal receptacle form is illustrated by Figures 155 to 171. The Tehachapi Mountain and Kernville specimens have shorter receptacle stalks and fewer loops per stalk than other specimens elsewhere. The centrally located populations (Baldwin Hills, Pacific Palisades, Las Barras Canyon, Limekiln Canyon, Chatsworth, and Placerita) all have a dense cluster of short stout setae at the anterior median edge of the carapace, while

all other populations have at most only a few very small or moderately stout setae here.

The similar geographic variation patterns for both sexes of *A. thompsoni* indicate two areas of reduced gene flow; one between the northeastern populations (Tehachapi Mountain and Kernville) and the rest of the species, and the other between the southeastern populations (Sierra Madre, Eaton Canyon, and Henninger Flats) and the rest of the species. In the former area it is likely that there is a paucity of suitable habitats. It is not as apparent why there might be reduced gene flow in the latter area. One female that was collected with the Tehachapi Mountain population looks suspiciously like a product of interbreeding between *A. thompsoni* and *A. torridus* or *A. plutonis*. If hybridization has occurred in this area, it could be responsible for some of the variant nature of the Tehachapi and Kernville populations.

A possible central Sierran population of A. thompsoni. Seven *Aliatypus* females with only a faint depression for a thoracic groove were collected at Mariposa, California (0.5 mi. north of town limits on Hwy. 49). These are similar to *A. thompsoni* in all characters execpt posterior sigilla size and separation and PTSR. The posterior sigilla of the Mariposa sample are markedly smaller (Fig. 33) and farther apart than in *A. thompsoni.* The PTSR of the Mariposa sample ranges from four to six with a mean of 4.3, while that of *A. thompsoni* ranges from five to eight with a mean of 6.2. Except for CL/PCL (Fig. 31) and the condition of the thoracic groove, this sample is even more similar to the sympatric species, *A. janus.* It is less similar to sympatric *A. californicus* and very unlike sympatric *A. erebus.*

There are a number of possible explanations for this situation. Perhaps this Mariposa sample is conspecific with *A. thompsoni.* Perhaps it is a reproductively isolated northern derivative of *A. thompsoni.* Perhaps it is a variant population of *A. janus* which has undergone a drastic shift in pars cephalica and thoracic groove structure. Perhaps it is a product of hybridization between *A. thompsoni* and *A. janus.* Intensive field work in the Mariposa area is required to solve this problem.

Distribution. Foothills of the Los Angeles area north into the Santa Ynez Mountains in the west and the southern end of the Sierra Nevada Mountains in the east (Map 4).

Records. CALIFORNIA. *Kern Co.:* Piute Mtns. S of Kernville, ♀. — along Water Canyon Rd., 4500-5500 ft., Tehachapi Mtns. S of

Tehachapi, 7 Sept. 1967, (♂); 10 Oct. 1968, 2 ♂, 2 ♀; 16 Jan. 1970, ♂; ♀. *Los Angeles Co.:* Sierra Madre, 900 ft., 4 Feb. 1973, ♂; ♀. —Eaton Canyon Park near Altadena, 8 ♀. — Henninger Flats near Altadena, 15 Nov. 1968, 2 ♂, 2 ♀; 10 Jan. 1968, ♂; 16 Jan. 1970, ♂; 10 ♀. — Las Barras Canyon, 2 mi. SE of Tujunga, 1500 ft., 12 Oct. 1972, 2 ♂, ♀. — Baldwin Hills, 2 ♀. — Pacific Palisades, Feb. 1945, ♂, ♀. — Chatsworth, 1000-1200 ft., 2 Oct. 1966, ♂; 9 Oct. 1966, ♂, 2 ♀; 28 Oct. 1967, ♂, ♀; 25 Nov. 1967, ♂, 3 ♀; 9 ♀. — Limekiln Canyon, 2.5 mi. NW of Granada Hills, 1300 ft., 3 ♀. — Placerita Canyon St. Pk., 31 Oct. 1968, 3 ♂, 5 ♀; 6 ♀. *Santa Barbara Co.:* Santa Ynez Mtns., Stagecoach Rd., 200 yds. W of junc. with Hwy. 154, 2200 ft., 5 ♀. — Santa Ynez Mtns., Paradise Rd. 2.1 mi. E of junc. with Hwy. 154, ♀. *Ventura Co.:* 5 mi. S of Squaw Flat, 2 ♀.

Aliatypus trophonius new species

Figures 61, 74, 87, 95, 116, 172-173. Map 4.

Type specimens and etymology. Holotype male from 4.5 mi. north of Soquel, Santa Cruz Co., California, 13 October 1971 (W. R. Icenogle). One male and nine female paratypes. Trophonius was a Boetian oracular god who snatched inquirers underground to give them revelations.

Diagnosis. Males: The palpus of this species (Fig. 116) is quite different from that of all other species, except *A. erebus* and *A. plutonis.* The OCS is quite broad to near the tip where it suddenly tapers to a fine point. Because of proportionately short appendage articles, a strongly swollen pedipalpal tibia (Fig. 87), and relatively large close-set anterior median eyes, any one of the following ratios (Table 1) will separate *A. trophonius* from nearly all other species: CL/IFL, CL/ITL, CL/IML, CL/PPL, PTT/PTL, CL/PTT, CL/AMD. *A. trophonius* is small, so that many dimensions, especially PFL and PTL (Table 1) are useful diagnostically. The most similar species, *A. erebus,* can be separated from *A. trophonius* best with the following ratios (Table 1) CL/PCA, CL/ITarL, and CL/AMD. Also, *A. trophonius* has a proportionately shorter proximal branch of the ICS base (Fig. 116) and a relatively broader conductor just proximal to the conductor tip than does *A. erebus. Females: A. trophonius* has relatively short leg I articles and relatively large, close spaced, posterior sigilla, so that it can be separated from any species by using the appropriate ratio from among the following (Table 2): IFL/IVFL, CL/IFL, CL/ITL, CL/IML,

SW/PSS, SW/PSL, and PSL/PSS. Small *A. trophonius* is easily separated from large species by IFL, ITL, and IML (Table 2). Closely related *A. erebus* can be distinguished from *A. trophonius* by the ratios (Table 2) CL/IMS, CL/AMD, and CL/PTSR, by body size (CL and other measurements in Table 2), and by the proportionately longer *A. trophonius* seminal receptacle stalks with more bends and relatively smaller bulbs (Figs. 172-173). *A. trophonius* seminal receptacles are also markedly different from those of several other species.

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep circular to elongate-oval pit. Postocular setae form roughly triangular grouping. *Sternum.* Fig. 61. Posterior sigilla medium sized and rather well separated. *Pedipalps.* Figs. 87, 116. Articles relatively short. Tibia greatly swollen ventrally, especially near distal end. Embolus base well separated from ICS base. OCS broad to near its tip where it suddenly tapers to fine point. Inner (concave) edge of OCS smooth. *Leg I.* Fig. 95. Majority of ventral macrosetae on tibia and metatarsus are ensiform; background setae fairly sparse, long and slender, more erect on metatarsus. *Abdomen.* Tergites I and III reduced to spots at bases of macrosetae. *Coloration.* Pars thoracica pale yellow. Pars cephalica darker; light brown to medium brown around margins and along median longitudinal line, lighter elsewhere. Chelicerae and pedipalps dorsally like pars cephalica.

Females: Carapace. Thoracic groove a deep pit; roughly circular or slightly transverse. Postocular setae form longitudinal triangular band. *Sternum.* Fig. 74. Posterior sigilla moderately large and somewhat elongate. Peripheral sternal setae slender. Longest setae scattered rather evenly over sternum. *Genitalia.* Figs. 172-173. Stalks of seminal receptacles very weakly sclerotized, only slightly more sclerotized than bulbs. Stalks moderately long and slender; about same diameter throughout length; with 3 to 5 bends. Bulbs proportionately small to medium sized. *Coloration.* Pars thoracica pale yellow to pale yellow-brown. Pars cephalica darker; light brown to medium red-brown around margins and along median longitudinal line, lighter elsewhere. Chelicerae like darkest part of pars cephalica.

Distribution. Known only from the low foothills of the Coast Range just west and south of San Francisco Bay (Map 4).

Records. CALIFORNIA. *San Francisco Co.:* San Francisco, ♀. *Santa Cruz Co.:* 4.5 mi. N of Soquel center on Soquel-San Jose Rd., 300 ft., 13 Oct. 1971, 2 ♂, 9 ♀.

Aliatypus erebus new species
Figures 34-38, 62, 75, 88, 114-115, 174-187. Map 4.

Type specimens and etymology. Holotype male from Fossil Ridge on south side of Mt. Diablo, Alameda Co., California, 24 November to 5 December, 1970 (W. E. Azevedo). Three male and two female paratypes. Erebus was the Latin god of darkness.

Diagnosis. Males: The ratios CL/PED and CL/PCA (Table 1) will separate *A. erebus* males from those of the closely related species, *A. trophonius, A. plutonis,* and *A. torridus.* For other characters useful in separating *A. erebus* from each of these species, see their diagnoses. *A. erebus'* conductor form (Figs. 114-115) and strongly swollen pedipalpal tibia (Fig. 88) are distinct from that of most other species. The ratios PTT/PTL, CL/ITarL, CL/IFL, CL/PED, and CL/PSL (Table 1) best distinguish *A. erebus* from the less closely related species. *Females: A. erebus'* seminal receptacles, with large bulbs and short stalks with normally only two (at most three) bends (Figs. 174-187), are distinct from those of all species except *A. torridus.* CL/PSL, SW/PSL, or PSL/PSS (Table 2) will separate *A. erebus* specimens nicely from distantly related species. CL/IMS, IMS/PSS, CL/PTSR, PTSR, or IMS (Table 2) distinguish *A. erebus* from *A. thompsoni.* CL/IMS, CL/AMD, CL/PTSR, CL, and IVTarL (Table 2) distinguish *A. erebus* from closely related *A. trophonius.* IVFL/IVML and CMT (Table 2) best distinguish *A. erebus* from closely related *A. plutonis.* CMT, CL/OQW, CL/CMT, and IMS/CMT (Table 2) are the most helpful characters when separating *A. erebus* specimens from those of very similar *A. torridus.*

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep circular or elongate oval pit; somewhat narrowed posteriorly. Postocular setae numerous and form a roughly triangular grouping. *Sternum.* Fig. 62. Posterior sigilla large and well separated. *Pedipalps.* Figs. 88, 114-115. Pedipalpal tibia robust; greatly swollen ventrally near distal end. Embolus base well separated from ICS base. Proximal branch of ICS base elongate. OCS rather broad to near its end where it quickly tapers to a fine point. Inner (concave) edge of OCS smooth to very rough. *Leg I.* Ventral tibia and metatarsal macrosetae attenuate and ensiform; background setae rather elongate and not closely appressed. *Abdomen.* Tergites I and III reduced to patches or spots at bases of macrosetae. *Coloration.* Pars thoracica grey-yellow. Pars cephalica markedly darker; medium brown to dark

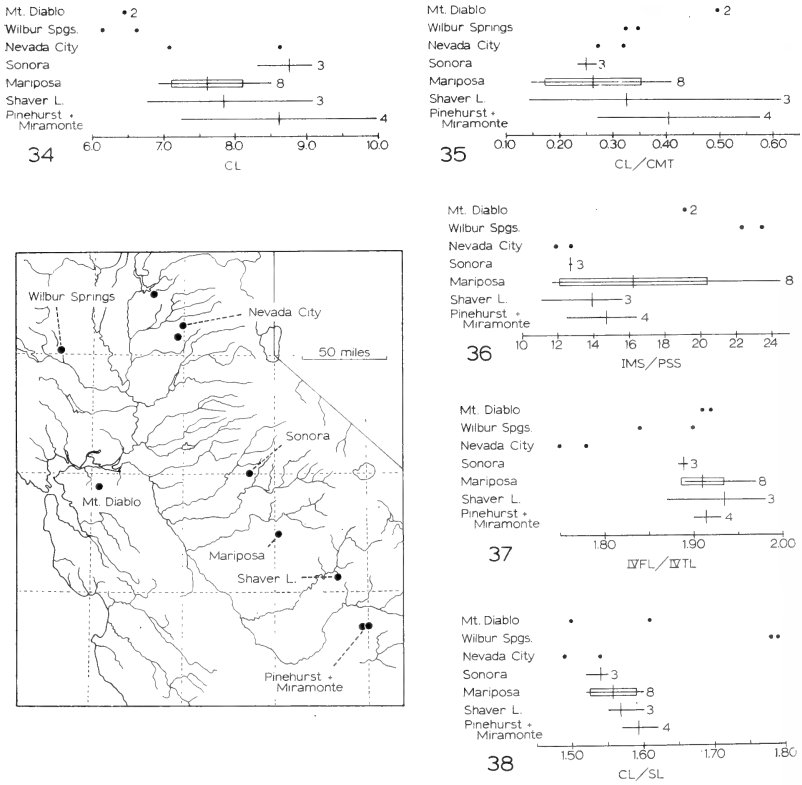
red-brown. Chelicerae match pars cephalica. Pedipalps dorsally like or slightly lighter than pars cephalica.

Females: Carapace. Thoracic groove a deep pit; elongate or transverse; rounded or triangular. Postocular setae numerous; form an elongate, roughly triangular grouping. *Sternum.* Fig. 75. Posterior sigilla large and rather well separated. Stout setae usually distributed around entire periphery of sternum; always common along anterior lateral margins. Most of central setae extremely elongate. *Genitalia.* Figs. 174-187. Seminal receptacles very weakly sclerotized. Stalks rather short; with 1 to 3 strong bends; same diameter throughout length. Bulbs large to very large. *Coloration.* Pars thoracica grey-yellow to pale brown. Pars cephalica darker; pale brown to dark chestnut brown; darkest along margins and median longitudinal line. Chelicerae light brown to dark chestnut brown.

Variation. Males: The two male samples, which are separated by the Central Valley, differ considerably in body size and EGS number but are very similar in most ratio characters. The male from Tuolumne Co. is markedly larger (CL = 6.6 mm), has a proportionately longer pedipalpal patella (CL/PPL = 1.57; PTL/PPL = 1.02) and metatarsus I (CL/IML = 1.76; IML/ITarL = 1.96), and proportionately closer posterior sigilla (SW/PSS = 5.41) than does the Mt. Diablo sample (CL = 4.4 mm-4.9 mm; CL/PPL = 1.94-2.03; PTL/PPL = 1.13-1.16; CL/IML = 1.94-2.07; IML/ITarL = 1.66-1.71; SW/PSS = 3.30-4.35). The only marked difference in palpus form is in conductor tip shape (Figs. 114-115).

Females: The four population samples from the southern half of the Sierra Nevada Mountains (Sonora, Mariposa, Shaver Lake, and Pinehurst-Miramonte) are similar in all characters. Each of the other three samples (Mt. Diablo, Wilbur Springs, and Nevada City) are divergent from this homogeneous south Sierra grouping in some characters. Of these divergent samples, the Mt. Diablo sample is less divergent than either the Wilbur Springs or Nevada City samples.

The Mt. Diablo sample is divergent from the south Sierra grouping in body size (Fig. 34), IFL/IVFL, and IFL/ITarL, and is somewhat divergent from all samples in CL/CMT (Fig. 35) and IMS/CMT. The Wilbur Springs sample is divergent from the south Sierra grouping in body size (Fig. 34), CL/SL (Fig. 38), CL/SW, ITL/IML, and IMS/PSS (Fig. 36), and is divergent from all samples in CL/SL (Fig. 38), CL/SW, and IMS/PSS (Fig. 36). The Nevada City sample is divergent from the south Sierra group-



Figures 34-38: Geographic variation of *Aliatypus erebus* females. Modified Dice-Leraas diagrams and map of sample localities. 34: CL (in mm) variation. 35: CL/CMT variation. 36: IMS/PSS variation. 37: IVFL/IVTL variation. 38: CL/SL variation.

ing in IVFL/IVTL (Fig. 37), IFL/IVFL, IVTL/IVML, and ITL/IML, and is divergent from all samples in IVFL/IVTL (Fig. 4) and ITL/IML. Mt. Diablo, Sonora, Mariposa, Pinehurst, and (two of three) Shaver Lake specimens have stout setae distributed all around the margins of the sternum. The Wilbur Springs, Nevada City, Miramonte, and (one of three) Shaver Lake specimens have only a few stout marginal setae, and these only at the anterior lateral sternal margins. In addition, the Wilbur Springs specimens are unique in not having short stout setae scattered over the periphery of the central region of the sternum. The range of color variation is considerable, with the Sonora specimens darkest, the Pinehurst and

Miramonte specimens a bit lighter, and all other specimens noticeably lighter than these. Variation in seminal receptacle form (Figs. 174-187) is continuous with no divergent populations. Bulb size and stalk diameter seem to be the most variable aspects of seminal receptacle form.

More and larger samples are needed before firm conclusions can be made about the genetic relationships of these populations. I feel that the best working hypothesis suggested by this analysis of variation is that the Mt. Diablo, Wilbur Springs, and Nevada City populations are, because of distance and ecological barriers to gene flow, markedly different genetically from the south Sierra populations, but that this isolation is either incomplete or has not been of long enough duration for reproductive isolating mechanisms to develop. A thorough search for more populations is especially needed in central and northern California in the eastern part of the Coast Range, the Central Valley, and the western foothills of the Sierra Nevada Mountains.

Distribution. Eastern edge of the Coast Range in central California and western slope of the Sierra Nevada Mountains (Map 4).

Records. CALIFORNIA. *Butte Co.:* 16 mi. E of Oroville on Lumpkin Rd., 1300 ft., ♀. *Colusa Co.:* 3 mi. SE of Wilbur Spgs. on Bear Cr. Rd., 1250 ft., 2 ♀. *Contra Costa Co.:* south side of Mt. Diablo, Fossil Ridge, 31 Oct.-6 Nov. 1970, ♂; 24 Nov.-5 Dec. 1970, 2♂; 5 Dec. 1970-20 Feb. 1971, ♂. — 0.5 mi. E of South Gate of Mt. Diablo St. Pk., 1300 ft., 2♀. *Fresno Co.:* Shaver Lake, 2♀. — Hwy. 168, 1.5 mi. S of Dinkey Cr. Rd., near Shaver Lake, 5400 ft., ♀. — Hwy. 245, 1 mi. E of Pinehurst, 4500 ft., 3♀. — Mt. Miramonte, ♀. *Mariposa Co.:* 0.5 mi. NW of Mariposa along Hwy. 49, 2000 ft., 8♀. *Nevada Co.:* Hwy. 49, 10.7 mi. S of Grass Valley, 1300 ft. — Hwy. 20, 2 mi. NE of Nevada City, 3000 ft., 2 ♀. *Tuolumne Co.:* Draper Mine Rd., 6 mi. E of Sonora, 2700 ft., 3♀. — probably near Sonora, summer 1968, ♂.

Aliatypus plutonis new species

Figures 63, 76, 89-90, 94, 117-118, 188-191. Map 4.

Type specimens and etymology. Holotype male from University of California at Riverside campus, Riverside Co., California, 31 October 1968 (W. R. Icenogle). One male and four female paratypes. The specific name is the genitive of Pluto, the Latin god of the nether world.

Diagnosis. Males: A. plutonis can be distinguished best from closely related and sympatric *A. torridus* by pedipalp and palpus

characters. The pedipalpal patella of *A. plutonis* is distinctively more elongate (Figs. 89-90; PPL/PFL and PTL/PPL in Table 1), its pedipalpal tibia has a distinctively different shape (Figs. 89-90; PTX/PTL in Table 1), and its OCS is drawn out into a broad thin lateral keel just below the tip (Figs. 117-118). *A. plutonis* can be distinguished from closely related but allopatric *A. erebus* by the following characters (Table 1): CL/PCA, CL/PED, CL/IFL, and the broad, thin OCS keel (Figs. 117-118). The following ratios will separate *A. plutonis* specimens from those of the other species: PSL/PSS, CL/PSL, CL/ITL, and CL/PPL (Table 1). *Females: A. plutonis* females are distinct from those of all other species by virtue of their low IVFL/IVML value (Table 2). This is the best character to use in separating *A. plutonis* from its closest relatives, *A. erebus* and *A. torridus*. The seminal receptacle stalks of *A. plutonis* are more elongate and more slender (Figs. 188-191) than those of *A. torridus* or *A. erebus*. SW/PSS and PSL/PSS (Table 2) are useful in separating *A. plutonis* from most of the other species.

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep pit, longer than wide; anterior border rounded; narrow posteriorly. Postocular setae usually form a double row anteriorly. *Sternum.* Fig. 63. Posterior sigilla large and moderately well separated. *Pedipalps.* Figs. 89-90, 117-118. Tibia strongly swollen ventrally near distal end; slightly swollen more proximally. Embolus base distant from ICS base. Conductor tip very sharp. Thin lateral keel-like extension of conductor (OCS) just proximal to tip so that conductor is markedly narrower just proximal of this keel. Inner (concave) edge of OCS smooth to slightly rough. *Leg I.* Fig. 94. Tibia and metatarsus with ventral, erect, elongate, attenuate and ensiform macrosetae; background setae elongate and not closely appressed. *Abdomen.* Tergites I and III reduced to small patches or spots at bases of macrosetae. *Coloration.* Pars thoracica grey-yellow to light brown. Pars cephalica darker, at least along margins and median longitudinal line; pale brown to medium brown. Chelicerae match lighter or darker portion of pars cephalica. Pedipalps dorsally like pars thoracica.

Female: Carapace. Thoracic groove a large deep pit; usually roughly triangular with front wall straight or procurved. Postocular setae distribution variable; single or roughly double longitudinal row or long narrow triangular grouping. *Sternum.* Fig. 76. Posterior sigilla large and moderately well separated. Stout setae distributed around entire periphery of sternum. Most of central setae

extremely elongate. *Genitalia.* Figs. 188-191. Seminal receptacles very weakly sclerotized. Stalks rather short, with a few strong loops (3-5 bends), moderately thick, and same diameter throughout length. Bulbs rather large. *Coloration.* Pars thoracica grey-yellow. Pars cephalica darker; light brown to medium brown; darkest along margins and median longitudinal line. Chelicerae match darkest parts of pars cephalica.

Variation. Males: Both Riverside males have a more slender pedipalpal tibia (Fig. 90) than all other specimens, which are all similar to Figure 89. The palpus form of most specimens is like Figure 118 or intermediate between this and the Palomar Mountain specimen (Fig. 117). *Females:* As illustrated (Figs. 188-191), there is a small amount of largely intrapopulation variation in bulb size and stalk diameter.

Distribution. Southwestern California south of the San Bernardino Mountains (Map 4).

Records. CALIFORNIA. *Riverside Co.:* U. of Calif. at Riverside campus, 1250 ft., 27 Oct. 1967, ♂; 31 Oct. 1968, ♂; 4♀. — S of Banning on Hwy. 243, 5.4 mi. S of junc. with I-10, 3300 ft., 21 Aug. 1968, (2♂), ♀; 3 ♀. *San Diego Co.:* Hwy. 395, 4 mi. E of Fallbrook, 800 ft.; 20 Sept. 1971, ♂. — Palomar Mtn., Nate Harrison Grade Rd., 2350 ft., 6 Jan. 1972, ♂.

Aliatypus torridus new species

Figures 64, 77, 91, 119-120, 192-194. Map. 4.

Type specimens and etymology. Holotype male from Mountain Center, Riverside Co., California, 3 October 1968 (W. R. Icenogle). One male and four female paratypes. The specific name is a Latin adjective meaning dry and hot.

Diagnosis. Males: The pedipalpal tibia (Fig. 91) of this species has a distinctive shape and the pedipalpal patella is relatively short so that PTX/PTL and PTL/PPL (Table 1) together distinguish *A. torridus* from all other species. For other characters which also distinguish *A. torridus* from closely related *A. trophonius, A. erebus,* and *A. plutonis,* see these species' diagnoses. *Females: A. torridus* is difficult to distinguish from *A. erebus;* CMT number, CL/OQW, CL/CMT, and IMS/CMT (Table 2) are the most helpful diagnostic characters. *A. torridus* is distinguished from closely related and sympatric *A. plutonis* by IVFL/IVML, PSL/PSS (Table 2), and its shorter, thicker seminal receptacle stalks (Figs. 192-194). Among the following characters can be found at least one that will

distinguish *A. torridus* from any one of the other *Aliatypus* species (Table 2): PSL/PSS, CL/PSL, CL/IFL, and seminal receptacle form (Figs. 192-194).

Description. See Tables 1-3.

Males: Carapace. Thoracic groove a deep pit with front wall broad and procurved; transverse to slightly longer than wide; narrowed posteriorly. Postocular setae grouped in form of narrow triangle. *Sternum.* Fig. 64. Posterior sigilla rather large and well separated. *Pedipalp.* Figs. 91, 119-120. Tibia swollen ventrally over most of its length. Embolus base distant from ICS base. Inner (concave) edge of OCS smooth to slightly rough. *Leg I:* Tibia and metatarsus setation very similar to that of *A. plutonis*. *Abdomen.* Tergites I and III reduced to small spots at bases of macrosetae. *Coloration.* Pars thoracica grey-yellow to pale brown. Pars cephalica darker; light brown to medium brown; darkest along margin and median longitudinal line. Chelicerae match either lighter or darker portion of pars cephalica. Pedipalps dorsally like pars thoracica.

Females: Carapace. Thoracic groove a large, deep, roughly triangular pit with transverse anterior wall; usually wider than long. Postocular setae form a long slender triangular grouping. *Sternum.* Fig. 77. Posterior sigilla large and well separated. Stout setae distributed around entire periphery of sternum. Most of central setae extremely elongate. *Genitalia.* Figs. 192-194. Seminal receptacles weakly to very weakly sclerotized. Stalks short, with 1 to 3 bends, thick, and same diameter throughout length. Bulbs rather large. *Coloration.* Pars thoracica pale yellow to pale brown. Pars cephalica darker; grey-yellow to medium brown; darkest along margins and median longitudinal line. Chelicerae medium brown.

Variation. Males: Considering the large geographic distance separating the two population samples, there is surprisingly little difference in pedipalp and palpus form (Figs. 119-120). Moderately strong differences between these two small samples show up only in the following ratios: CL/ALS (El Paso Mountain sample with higher mean), CL/ITL (Mountain Center mean higher), and IFL/ITarL (El Paso Mountain mean higher).

Females: Seminal receptacle form is remarkably similar throughout all three population samples (Figs. 192-194). Noteworthy geographic variation occurs in five ratio characters. The Yucaipa sample ($n = 2$) has markedly smaller mean values of IMS/CTP and CL/CTP than both the Mountain Center ($n = 4$) and El Paso Mountain ($n = 2$) samples. In three other characters, CL/OQW,

CL/AMD, and IFL/ITL, the Mountain Center and El Paso samples are markedly different from one another and the Yucaipa sample is intermediate.

Distribution. Interior southern California from the San Jacinto Mountains north to the southern Sierra Nevada Mountains (Map 4).

Records. CALIFORNIA. *Kern Co.:* NE edge of El Paso Mtns., 1 mi. W of Hwy. 395, 3800 ft., 3 Jan. 1969, 2♂; 2♀. — NE of El Paso Mtns., spring 1963, ♂. *Riverside Co.:* Mountain Center, 300 yds. W of junc. of Hwys. 243 and 74, 4400 ft., 3 Oct. 1968, 2♂; 4♀. *San Bernardino Co.:* Yucaipa, 2800 ft., 2♀.

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Table 1. Measurement (in mm), meristic character, and diagnostic ratio values for adult males of Aliatypus species. For each species or group of species, the most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurements and ratios. Range and mean given for EGS. Character abbreviations are defined in Methods section.

	N	CL	PCL	CW	IFL	ITL	IML	ITarL
californicus	14	3.2-5.9 4.73±.74	1.92-3.38 2.728±.427	2.50-4.58 3.723±.596	3.15-5.27 4.373±.602	2.04-3.61 2.864±.423	2.04-3.58 2.901±.440	1.19-1.92 1.601±.216
janus	12	4.0-5.7 5.15±.53	2.30-3.38 2.997±.324	2.96-4.69 4.085±.485	3.77-5.85 5.078±.548	2.23-3.61 3.110±.352	2.61-3.81 3.394±.327	1.27-1.77 1.612±.146
isolatus	4	3.5-4.9 4.26	2.15-2.92 2.517	2.88-4.08 3.487	3.50-5.08 4.317	2.15-3.23 2.700	2.38-3.42 2.950	1.15-1.61 1.407
aquilonius	4	2.8-3.1 2.87	1.53-1.69 1.610	2.27-2.46 2.343	2.92-3.19 3.037	1.77-1.92 1.830	1.92-2.07 1.997	1.03-1.07 1.057
gnomus	2	3.1-3.4 3.25	1.77-2.00 1.885	2.54-2.77 2.655	2.92-3.31 3.115	1.96-2.15 2.055	1.96-2.19 2.075	1.07-1.15 1.110
gulosus	5	3.2-3.7 3.47	1.84-2.15 2.010	2.65-3.04 2.868	3.46-4.85 3.606	2.27-2.42 2.350	2.30-2.57 2.458	1.42-1.61 1.534
thompsoni	19	3.4-4.9 4.23±.53	2.30-3.07 2.734±.234	2.84-4.11 3.457±.369	3.92-5.85 4.978±.593	2.46-3.46 3.056±.329	2.92-4.35 3.717±.442	1.46-1.92 1.736±.141
trophonius	2	2.9-3.7 3.30	1.69-2.15 1.920	2.27-2.84 2.555	2.27-2.77 2.520	1.38-1.65 1.515	1.53-1.92 1.725	0.92-1.15 1.035
erebus	5	4.4-6.6 5.09	2.54-3.77 2.973	3.46-5.46 4.037	3.39-5.31 3.974	2.04-3.23 2.378	2.24-3.77 2.651	1.35-1.92 1.512
plutonis	6	4.1-4.5 4.25±.127	2.38-2.54 2.473±.079	3.27-3.54 3.408±.097	3.84-4.31 3.985±.189	2.19-2.57 2.310±.147	2.34-2.84 2.515±.182	1.30-1.53 1.412±.090
torridus	5	3.8-4.6 4.20	2.30-2.61 2.442	3.07-3.73 3.380	3.54-4.31 3.956	2.00-2.57 2.334	2.30-2.77 2.550	1.27-1.46 1.374

	PFL	PPL	PTL	PTX	PTT	PED	PCA
californicus	4.08-6.73 5.271±.961	2.34-4.31 3.284±.583	2.65-4.92 3.794±.676	1.92-3.77 2.761±.535	0.62-1.07 0.898±.151	0.81-1.36 1.142±.198	0.36-0.75 0.571±.129
janus	3.92-6.73 5.466±.849	2.30-3.96 3.260±.488	2.69-5.00 3.930±.734	2.00-3.92 3.021±.623	0.77-0.99 0.911±.073	0.92-1.51 1.211±.164	0.36-0.66 0.537±.083
isolatus	3.73-5.62 4.665	2.00-3.11 2.575	2.61-4.00 3.325	2.15-3.15 2.592	0.66-0.90 0.777	0.92-1.33 1.142	0.40-0.59 0.495
aquilonius	2.96-3.23 3.087	2.04-2.15 2.087	2.11-2.27 2.177	1.53-1.61 1.557	0.48-0.49 0.487	0.75-0.83 0.783	0.36-0.44 0.400
gnomus	3.07-3.54 3.305	1.84-2.04 1.940	2.23-2.50 2.365	1.61-1.84 1.725	0.53-0.55 0.540	0.73-0.77 0.750	0.31-0.33 0.320
gulosus	3.29-4.23 4.092	2.38-2.69 2.506	3.46-3.69 3.584	1.38-1.61 1.532	0.62-0.68 0.640	0.64-0.68 0.652	0.31-0.33 0.314
thompsoni	3.69-5.92 4.779±.636	2.34-3.88 3.111±.479	2.65-4.04 3.291±.380	1.92-3.07 2.437±.314	0.64-0.99 0.832±.099	0.92-1.27 1.148±.097	0.44-0.73 0.626±.083
trophonius	2.19-2.65 2.420	1.38-1.69 1.535	1.69-1.92 1.805	1.23-1.38 1.305	0.64-0.81 0.725	0.73-0.86 0.795	0.44-0.53 0.485
erebus	3.46-6.19 4.169	2.27-4.23 2.745	2.62-4.31 3.040	1.85-3.31 2.234	1.04-1.57 1.187	0.93-1.22 0.991	0.48-0.70 0.543
plutomis	4.15-4.85 4.435±.254	2.77-3.23 2.942±.166	3.15-3.73 3.345±.202	2.30-2.92 2.497±.223	0.81-0.96 0.897±.071	0.99-1.16 1.055±.064	0.53-0.62 0.568±.035
torridus	3.69-4.54 4.168	2.11-2.65 2.426	2.77-3.50 3.190	1.77-2.30 2.102	0.79-0.90 0.830	1.01-1.12 1.058	0.55-0.61 0.574

Table 1 (continued)

	SL	SW	PSS	PSL	OQW	ALS	ALD
californicus	1.84-3.31 2.755±.421	1.50-2.65 2.195±.359	0.53-0.85 0.687±.102	0.18-0.36 0.264±.064	0.81-1.22 1.074±.117	0.35-0.66 0.526±.075	0.24-0.35 0.271±.029
janus	2.23-3.46 3.059±.373	1.84-2.81 2.417±.299	0.55-0.98 0.776±.130	0.20-0.36 0.289±.053	0.86-1.27 1.129±.118	0.36-0.61 0.536±.073	0.24-0.33 0.289±.029
isolatus	2.07-2.92 2.515	1.73-2.34 2.062	0.62-0.81 0.715	0.20-0.25 0.212	0.92-1.22 1.065	0.46-0.62 0.540	0.22-0.27 0.240
aquilonius	1.46-1.69 1.560	1.30-1.38 1.327	0.55-0.64 0.587	0.09-0.12 0.097	0.73-0.81 0.743	0.35-0.44 0.383	0.20-0.22 0.200
gnomus	1.77-1.92 1.845	1.38-1.61 1.495	0.61-0.62 0.615	0.12 0.120	0.83-0.85 0.840	0.40-0.44 0.420	0.22-0.25 0.235
gulosus	1.92-2.15 2.042	1.61-1.84 1.704	0.57-0.73 0.658	0.11-0.16 0.146	0.90-0.98 0.942	0.42-0.49 0.460	0.22-0.25 0.236
thompsoni	1.92-2.84 2.437±.271	1.88-2.46 2.112±.208	0.16-0.40 0.255±.074	0.36-0.55 0.452±.058	0.83-1.18 0.988±.100	0.40-0.62 0.511±.061	0.22-0.29 0.245±.021
trophonius	1.61-2.00 1.805	1.42-1.80 1.610	0.48-0.55 0.515	0.20-0.29 0.245	0.81-0.98 0.895	0.44-0.55 0.495	0.18-0.25 0.215
erebus	2.54-3.92 2.958	2.00-3.46 2.502	0.46-0.64 0.595	0.35-0.75 0.506	1.07-1.49 1.172	0.57-0.81 0.658	0.24-0.33 0.283
plutonis	2.38-2.46 2.407±.041	2.04-2.23 2.132±.072	0.42-0.57 0.487±.050	0.36-0.44 0.393±.027	1.05-1.16 1.103±.039	0.59-0.64 0.607±.021	0.25-0.33 0.273±.032
torridus	2.30-2.69 2.456	1.96-2.30 2.090	0.49-0.64 0.552	0.31-0.40 0.356	1.03-1.31 1.152	0.49-0.64 0.578	0.24-0.35 0.300

	AMS	AMD	EGS	CL/IFL	CL/ITL	CL/IML	CL/ITarL	CL/PPL
californicus	0.10-0.21 0.158±.029	0.12-0.18 0.149±.020	6-34 20.1	1.03-1.15 1.080±.043	1.56-1.78 1.652±.079	1.57-1.73 1.631±.049	2.69-3.22 2.951±.153	1.33-1.61 1.447±.082
janus	0.15-0.19 0.171±.013	0.09-0.16 0.132±.020	20-57 28.4	0.95-1.08 1.016±.043	1.52-1.79 1.662±.102	1.39-1.59 1.518±.061	2.79-3.44 3.197±.177	1.28-1.90 1.599±.187
isolatus	0.12-0.16 0.145	0.12-0.16 0.140	20-33 19.3	0.94-1.01 0.991	1.48-1.65 1.588	1.39-1.52 1.448	2.95-3.13 3.032	1.53-1.77 1.674
aquilonius	0.09-0.16 0.107	0.08-0.12 0.107	10-12 10.7	0.92-0.96 0.945	1.54-1.60 1.568	1.39-1.48 1.437	2.59-2.87 2.716	1.34-1.43 1.375
gnomus	0.12-0.13 0.125	0.11-0.12 0.115	10-12 11.0	1.02-1.05 1.035	1.56-1.57 1.565	1.54-1.57 1.555	2.87-2.94 2.905	1.66-1.67 1.665
gulosus	0.12-0.15 0.136	0.12-0.16 0.136	14-26 18.4	0.94-0.99 0.963	1.42-1.55 1.479	1.37-1.50 1.414	2.20-2.38 2.268	1.26-1.48 1.389
thompsoni	0.12-0.20 0.149±.030	0.10-0.15 0.128±.013	15-28 22.2	0.79-0.90 0.850±.034	1.23-1.52 1.384±.075	1.02-1.24 1.140±.061	2.21-2.78 2.433±.168	1.27-1.56 1.368±.084
trophonius	0.11-0.13 0.120	0.13-0.17 0.150	13-24 18.5	1.29-1.33 1.310	2.11-2.24 2.175	1.91-1.92 1.915	3.17-3.21 3.190	2.12-2.18 2.150
erebus	0.17-0.25 0.192	0.15-0.19 0.176	15-41 24.5	1.25-1.33 1.288	2.05-2.25 2.162	1.76-2.07 1.948	3.26-3.46 3.378	1.57-2.03 1.906
plutonis	0.15-0.22 0.182±.023	0.12-0.17 0.147±.016	14-22 16.3	1.03-1.08 1.068±.019	1.73-1.89 1.845±.062	1.57-1.78 1.696±.079	2.87-3.22 3.021±.149	1.38-1.53 1.449±.058
torridus	0.16-0.20 0.180	0.14-0.16 0.148	16-27 20.4	1.02-1.13 1.067	1.71-1.93 1.814	1.59-1.74 1.655	2.95-3.16 3.065	1.61-1.86 1.744

Table 1 (continued)

	CL/PTT	CL/PED	CL/PCA	CL/PSS	CL/PSL	CL/ALS	CL/AMD
californicus	4.72-5.79 5.291±.297	3.59-4.76 4.165±.338	6.83-11.47 8.472±1.218	5.93-9.51 6.947±1.085	13.6-21.5 18.38±2.40	7.84-10.74 9.005±.772	25.6-37.3 31.90±3.30
janus	5.13-6.26 5.654±.373	3.36-4.78 4.286±.390	7.70-11.11 9.718±1.098	5.81-7.59 6.720±.638	14.5-24.4 18.23±2.98	8.70-11.11 9.677±.677	31.7-46.1 39.50±4.30
isolatus	5.06-5.82 5.488	3.59-3.94 3.740	8.08-9.60 8.686	5.36-6.39 5.959	17.7-23.8 20.10	7.70-8.08 7.888	29.5-32.0 30.51
aquilonius	5.65-6.27 5.896	3.60-3.70 3.663	6.30-8.53 7.249	4.80-5.31 4.898	24.3-34.1 30.02	6.64-7.91 7.504	25.1-36.5 27.18
gnomus	5.79-6.15 5.97	4.21-4.39 4.300	9.30-10.90 10.100	4.95-5.54 5.245	25.5-28.1 26.87	7.68 7.68	27.9-28.1 28.04
gulosus	5.21-5.77 5.433	4.89-5.77 5.336	10.42-11.90 11.074	4.63-5.80 5.318	22.1-30.7 24.22	7.22-8.05 7.568	22.5-29.5 25.84
thompsoni	4.61-5.47 5.087±.204	3.37-4.39 3.681±.295	5.93-8.34 6.815±.788	11.86-24.60 17.455±3.554	8.0-10.7 9.40±.77	7.28-9.28 8.302±.529	28.1-43.3 33.19±3.74
trophonius	4.55-4.56 4.555	4.00-4.29 4.145	6.64-6.96 6.800	5.31-7.69 6.500	12.7-14.6 13.66	6.64-6.71 6.675	21.7-22.4 22.08
erebus	4.22-4.39 4.320	4.68-5.43 5.116	9.17-9.56 9.406	6.84-10.34 8.760	8.8-13.4 10.58	7.21-8.63 7.790	25.2-34.8 29.76
plutonis	4.32-5.51 4.778±.505	3.84-4.35 4.041±.190	7.19-7.83 7.500±.283	7.10-10.26 8.812±.852	9.8-11.7 10.85±.72	6.69-7.56 7.022±.349	25.3-34.6 29.28±3.05
torridus	4.86-5.33 5.077	3.80-4.12 3.977	6.74-8.11 7.340	6.97-8.47 7.666	10.3-14.4 11.93	6.00-8.47 7.383	27.4-29.6 28.46

	PSL/PSS	PPL/PFL	PTL/PPL	PTX/PTL	PTT/PTL	IML/ITarL	SW/PSS
californicus	0.28-0.64 0.391±.117	0.60-0.65 0.624±.019	1.01-1.21 1.155±.026	0.69-0.77 0.726±.022	0.21-0.25 0.237±.011	1.71-1.95 1.810±.074	2.77-4.33 3.218±.502
janus	0.24-0.51 0.380±.081	0.54-0.65 0.598±.040	1.07-1.31 1.202±.089	0.73-0.80 0.766±.022	0.19-0.29 0.237±.035	2.01-2.24 2.106±.088	2.76-3.64 3.142±.260
isolatus	0.25-0.32 0.299	0.54-0.56 0.551	1.26-1.33 1.295	0.73-0.82 0.783	0.21-0.27 0.236	2.06-2.13 2.095	2.62-3.03 2.882
aquilonius	0.14-0.22 0.166	0.67-0.69 0.676	1.03-1.06 1.043	0.71-0.73 0.715	0.18-0.23 0.224	1.86-1.93 1.889	2.16-2.51 2.267
gnomus	0.19-0.20 0.195	0.58-0.60 0.590	1.21-1.23 1.220	0.72-0.74 0.730	0.22-0.24 0.230	1.83-1.90 1.865	2.23-2.64 2.435
gulosus	0.15-0.26 0.225	0.60-0.64 0.612	1.37-1.46 1.431	0.37-0.45 0.428	0.17-0.19 0.179	1.53-1.73 1.605	2.21-2.90 2.610
thompsoni	1.28-2.38 1.864±.381	0.61-0.69 0.649±.021	0.95-1.20 1.065±.057	0.72-0.79 0.740±.017	0.23-0.27 0.253±.011	1.97-2.46 2.137±.122	5.91-12.50 8.792±2.068
trophonius	0.36-0.60 0.480	0.63-0.64 0.635	1.14-1.22 1.180	0.72-0.73 0.725	0.38-0.42 0.400	1.66-1.67 1.665	2.58-3.75 3.165
erebus	0.50-1.17 0.858	0.64-0.68 0.656	1.02-1.16 1.120	0.71-0.78 0.734	0.36-0.40 0.390	1.66-1.96 1.740	3.30-5.41 4.274
plutonis	0.67-1.05 0.819±.133	0.65-0.68 0.663±.009	1.10-1.16 1.137±.021	0.73-0.78 0.745±.022	0.22-0.29 0.270±.033	1.73-1.86 1.781±.048	3.91-5.21 4.414±.434
torridus	0.48-0.82 0.655	0.57-0.59 0.582	1.31-1.32 1.315	0.64-0.68 0.658	0.25-0.29 0.261	1.77-1.90 1.853	3.36-4.08 3.807

Table 2. Measurement (in mm), meristic character, and diagnostic ratio values for adult females of Aliatypus species. For each species or group of species, the most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurements and ratios. Range and mean given for meristic characters. Number of females containing maturing eggs or with brood is in parentheses after N. Character abbreviations are defined in Methods section.

	N	CL	PCL	CW	IFL	ITL	IML	ITarL
californicus	44(24)	5.4-8.0 6.66±.68	3.07-4.69 3.927±.408	3.88-6.04 4.963±.560	3.92-5.38 4.689±.462	2.30-3.31 2.796±.292	1.96-2.73 2.344±.229	1.00-1.34 1.139±.105
janus	25(13)	5.1-8.9 6.62±.92	3.07-5.38 3.973±.522	3.69-6.46 4.878±.675	3.42-6.27 4.756±.675	2.00-3.84 2.844±.461	1.77-3.00 2.382±.318	0.92-1.38 1.153±.125
isolatus	10(4)	4.6-8.3 5.71±1.05	2.77-5.00 3.475±.623	3.34-6.15 4.349±.775	3.00-5.69 3.860±.744	1.80-3.38 2.326±.432	1.50-2.84 1.948±.363	0.80-1.23 0.981±.121
aquilonius	26(12)	2.8-5.9 3.96±.84	1.61-3.38 2.354±.472	2.27-4.50 3.040±.621	1.84-3.73 2.536±.528	1.07-2.19 1.502±.319	0.88-1.84 1.263±.259	0.46-0.80 0.590±.104
gnomus	4(4)	3.5-4.2 3.77	2.07-2.46 2.227	2.46-3.07 2.717	2.30-2.81 2.497	1.38-1.65 1.485	1.19-1.42 1.285	0.57-0.69 0.630
gulosus	27(13)	4.8-7.7 6.07±.65	2.92-4.69 3.716±.380	3.58-5.62 4.613±.494	2.81-4.46 3.441±.342	1.61-2.61 2.024±.213	1.30-2.15 1.645±.171	0.76-1.15 0.915±.089
thompsoni	66(25)	4.8-7.9 6.28±.60	3.61-5.38 4.429±.416	3.77-5.85 4.679±.406	3.15-5.15 4.080±.393	1.77-2.92 2.331±.235	1.50-2.46 1.937±.185	0.84-1.23 1.041±.081
trophonius	10(6)	3.5-5.2 4.38±.55	2.15-3.23 2.691±.348	2.84-3.92 3.236±.477	1.84-2.84 2.336±.341	1.03-1.65 1.366±.206	0.88-1.34 1.129±.161	0.46-0.73 0.615±.087
erebus	24(6)	6.2-10.0 7.78±1.01	3.77-6.31 4.765±.614	4.54-7.54 5.949±.823	3.34-5.38 4.482±.609	2.00-3.23 2.700±.390	1.61-2.69 2.200±.330	0.84-1.27 1.065±.124
plutonis	8(6)	6.0-7.9 6.68±.53	3.69-4.61 4.075±.262	4.54-6.00 5.076±.417	3.61-4.77 4.065±.342	2.19-2.84 2.472±.194	1.88-2.30 2.079±.150	0.92-1.15 1.040±.085
torridus	8(3)	5.5-6.5 6.10±.32	3.38-4.00 3.759±.208	4.15-5.00 4.740±.297	3.27-3.92 3.656±.214	1.88-2.34 2.139±.145	1.57-1.88 1.761±.095	0.84-1.00 0.930±.056

	IVFL	IVTL	IVML	IVTarL	SL	SW	PSS
californicus	3.61-5.23 4.404±.439	2.07-3.07 2.571±.278	3.11-4.46 3.747±.373	1.15-1.53 1.341±.095	3.31-5.23 4.247±.450	2.69-4.15 3.431±.398	0.79-1.49 1.087±.167
janus	3.23-5.77 4.412±.597	1.92-3.46 2.639±.388	2.77-4.81 3.804±.529	1.07-1.50 1.314±.127	3.23-5.77 4.377±.575	2.54-4.46 3.415±.460	0.72-1.33 1.014±.170
isolatus	2.96-5.38 3.759±.669	1.77-3.15 2.224±.383	2.54-4.46 3.171±.518	0.92-1.53 1.154±.161	2.69-5.00 3.520±.641	2.38-4.04 2.994±.478	0.86-1.38 1.014±.148
aquilonius	1.92-3.69 2.550±.503	1.07-2.23 1.484±.312	1.57-3.07 2.121±.411	0.65-1.07 0.819±.128	1.69-3.54 2.369±.511	1.42-2.92 1.967±.414	0.61-1.01 0.722±.093
gnomus	2.30-2.77 2.487	1.38-1.65 1.485	1.96-2.27 2.085	0.80-0.96 0.880	2.07-2.38 2.245	1.69-2.04 1.845	0.66-0.75 0.692
gulosus	2.92-4.61 3.562±.360	1.57-2.46 1.933±.201	2.54-3.96 3.099±.302	1.00-1.46 1.183±.094	2.92-4.77 3.808±.421	2.46-3.88 3.293±.357	0.85-1.42 1.105±.135
thompsoni	3.07-4.65 3.873±.347	1.53-2.61 2.159±.213	2.57-4.19 3.333±.326	1.00-1.46 1.228±.084	2.92-4.77 3.824±.382	2.61-3.88 3.267±.278	0.18-0.46 0.357±.062
trophonius	2.07-3.07 2.554±.344	1.07-1.65 1.365±.188	1.96-2.65 2.175±.293	0.73-1.07 0.903±.104	2.00-3.23 2.550±.412	1.77-2.92 2.281±.383	0.42-0.64 0.539±.070
erebus	3.61-5.46 4.592±.569	1.92-2.84 2.424±.312	3.04-4.92 3.998±.539	1.19-1.61 1.437±.122	3.46-6.15 4.943±.705	2.92-5.23 4.282±.625	0.49-1.12 0.790±.163
plutonis	3.61-4.73 4.055±.322	1.92-2.50 2.214±.167	3.34-4.61 3.910±.356	1.27-1.42 1.312±.049	3.46-4.92 4.075±.407	3.23-4.27 3.586±.328	0.53-0.73 0.637±.066
torridus	3.31-3.92 3.661±.217	1.73-2.00 1.896±.093	2.84-3.46 3.185±.217	1.15-1.30 1.219±.061	3.46-4.31 3.882±.241	2.96-3.54 3.350±.196	0.55-0.77 0.714±.070

Table 2 (continued)

	PSL	OQW	ALS	ALD	AMS	AMD	CTP	CTR	CMT
californicus	0.29-0.59 0.387±.072	1.10-1.72 1.372±.151	0.55-0.98 0.742±.114	0.25-0.36 0.307±.031	0.16-0.29 0.220±.036	0.12-0.20 0.155±.020	7-12 8.3	3-7 4.6	6-36 19.2
janus	0.29-0.66 0.416±.089	0.99-1.68 1.308±.175	0.46-0.85 0.688±.101	0.24-0.38 0.302±.038	0.16-0.36 0.225±.045	0.11-0.18 0.130±.019	6-10 7.9	3-6 4.3	9-44 18.2
isolatus	0.18-0.38 0.277±.064	1.03-1.72 1.262±.199	0.51-1.01 0.678±.148	0.25-0.33 0.286±.036	0.17-0.36 0.220±.054	0.11-0.16 0.130±.017	7-12 8.7	3-6 4.3	11-27 16.0
aquilonius	0.09-0.29 0.160±.067	0.68-1.27 0.916±.173	0.33-0.72 0.503±.103	0.18-0.28 0.230±.026	0.11-0.22 0.142±.029	0.08-0.12 0.099±.011	6-8 7.0	3-5 3.5	6-16 10.0
gnomus	0.12-0.22 0.165	0.83-0.98 0.872	0.38-0.53 0.447	0.22-0.25 0.237	0.07-0.11 0.090	0.12-0.15 0.132	7 7.0	3-4 3.3	7-11 9.3
gulosus	0.22-0.55 0.357±.075	1.12-1.83 1.462±.154	0.61-1.10 0.792±.105	0.22-0.36 0.291±.031	0.21-0.36 0.289±.043	0.11-0.17 0.131±.014	6-9 7.3	3-4 3.1	7-20 12.3
thompsoni	0.55-1.10 0.737±.124	1.09-1.68 1.353±.142	0.53-0.94 0.728±.088	0.25-0.42 0.307±.031	0.12-0.35 0.221±.043	0.11-0.17 0.141±.014	6-10 7.4	3-6 4.2	7-42 14.4
trophonius	0.27-0.61 0.441±.096	0.98-1.40 1.147±.151	0.55-0.83 0.655±.092	0.22-0.33 0.261±.033	0.17-0.29 0.219±.047	0.12-0.16 0.133±.014	6-7 6.4	2-3 2.5	8-14 10.3
erebus	0.70-1.25 0.946±.156	1.38-2.25 1.750±.210	0.79-1.40 0.999±.146	0.29-0.38 0.333±.026	0.22-0.49 0.362±.070	0.12-0.18 0.153±.020	7-13 8.1	3-5 3.8	11-68 28.9
plutonis	0.70-0.96 0.827±.100	1.49-1.79 1.639±.095	0.86-1.10 0.976±.077	0.29-.036 0.316±.026	0.25-0.42 0.324±.055	0.13-0.17 0.147±.012	7-9 7.8	3-4 3.6	4-11 8.1
torridus	0.55-0.77 0.679±.082	1.47-1.84 1.646±.143	0.83-1.12 0.944±.087	0.29-0.36 0.321±.028	0.25-0.36 0.299±.032	0.14-0.17 0.156±.011	6-9 7.3	3-4 3.2	4-11 7.0

	PTSP	PTSR	IMS	CL/IFL	CL/ITL	CL/IML	CL/IVTL	CL/PSS	CL/PSL
californicus	4-9	4-7	12-20	1.28-1.53	2.16-2.61	2.60-3.22	2.31-2.86	4.7-7.7	12.3-21.9
	6.2	4.4	15.7	1.421±.055	2.384±.103	2.842±.126	2.595±.149	6.19±.65	17.53±2.26
janus	5-14	4-12	14-30	1.29-1.49	2.06-2.56	2.54-2.98	2.29-2.71	5.1-8.3	12.1-20.5
	6.8	5.1	20.8	1.394±.051	2.340±.121	2.782±.109	2.515±.094	6.62±.92	16.22±2.02
isolatus	5-7	4-6	14-28	1.44-1.54	2.35-2.48	2.82-3.07	2.47-2.64	5.0-6.4	14.9-33.2
	6.4	4.6	17.7	1.481±.031	2.456±.058	2.933±.080	2.563±.057	5.61±.43	21.38±5.34
aquilonius	5-8	4-8	11-14	1.49-1.61	2.52-2.77	2.98-3.34	2.50-2.78	4.4-6.8	17.5-41.0
	6.2	5.8	11.8	1.560±.036	2.636±.062	3.130±.090	2.666±.071	5.44±.62	26.82±6.07
gnomus	6	4	13-16	1.48-1.54	2.51-2.57	2.88-2.97	2.51-2.57	5.3-5.5	18.8-29.5
	6.0	4.0	14.5	1.510	2.539	2.932	2.539	5.43	23.74
gulosus	4-10	3-5	7-12	1.66-1.88	2.80-3.14	3.43-3.84	2.86-3.34	4.8-6.3	13.5-22.2
	5.7	4.0	9.4	1.763±.058	2.997±.083	3.689±.113	3.139±.120	5.50±.29	17.42±2.43
thompsoni	5-10	5-8	14-31	1.41-1.66	2.39-2.90	2.88-3.54	2.61-3.12	12.7-31.6	6.5-10.9
	6.3	6.2	19.8	1.541±.050	2.698±.096	3.246±.130	2.913±.112	18.14±3.57	8.65±.98
trophonius	6-7	3-5	11-12	1.79-1.96	3.06-3.44	3.67-4.02	3.06-3.42	7.2-9.9	8.5-13.1
	6.2	4.0	11.5	1.882±.052	3.221±.109	3.892±.106	3.218±.107	8.175±.83	10.16±1.28
erebus	4-7	3-4	11-14	1.56-1.87	2.61-3.23	3.15-3.92	2.96-3.52	7.7-14.7	6.5-9.8
	6.0	4.0	11.8	1.740±.089	2.891±.152	3.552±.202	3.211±.138	10.10±1.67	8.29±.72
plutonis	5-6	4-5	10-13	1.57-1.72	2.54-2.88	2.97-3.45	2.88-3.14	9.5-11.3	6.9-8.8
	5.9	4.3	12.3	1.643±.045	2.702±.106	3.214±.165	3.017±.106	10.51±.72	8.12±.64
torridus	6	4	11-15	1.60-1.71	2.67-2.95	3.34-3.65	3.08-3.36	8.0-10.0	8.3-10.0
	6.0	4.0	12.1	1.668±.034	2.854±.099	3.463±.098	3.215±.081	8.59±.65	9.05±.77

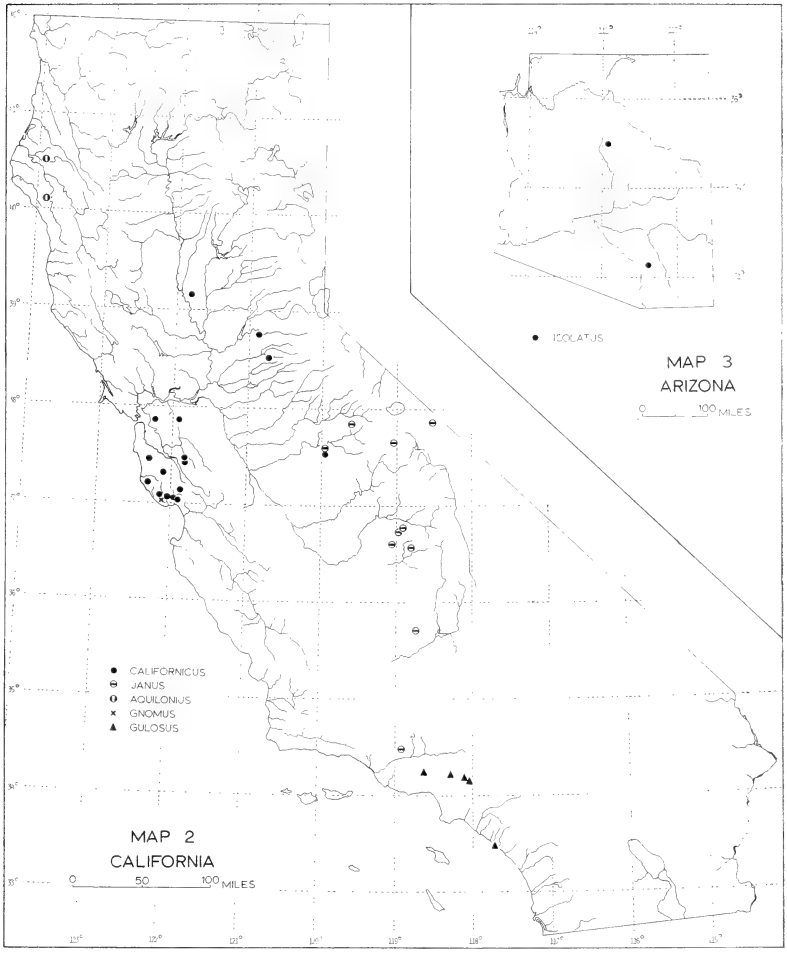
Table 2 (continued)

	CL/OQW	CL/AMD	CL/CMT	CL/PTSR	CL/IMS	IFL/IVFL	IVFL/IVML
californicus	4.30-5.44 4.862±.278	35.8-52.5 43.35±4.16	0.16-1.08 0.395±.177	0.97-1.96 1.539±.257	0.30-0.64 0.429±.064	1.02-1.13 1.065±.026	1.13-1.23 1.176±.024
janus	4.44-5.63 5.067±.276	41.0-63.7 51.06±5.37	0.16-0.87 0.426±.181	0.45-2.23 1.385±.377	0.22-0.53 0.333±.090	1.02-1.13 1.077±.024	1.11-1.23 1.161±.032
isolatus	4.12-4.83 4.513±.223	38.4-51.9 43.81±4.08	0.21-0.76 0.399±.159	0.95-2.08 1.274±.331	0.20-0.42 0.331±.058	1.01-1.06 1.025±.015	1.13-1.23 1.183±.034
aquilonius	3.79-4.61 4.306±.194	30.7-53.1 39.74±5.16	0.26-.64 0.416±.119	0.46-1.07 0.685±.162	0.22-0.53 0.338±.078	0.96-1.02 0.992±.014	1.17-1.25 1.202±.022
gnomus	4.16-4.63 4.323	27.2-29.5 28.48	0.35-0.51 0.417	0.89-1.04 0.942	0.24-0.28 0.260	1.00-1.01 1.004	1.17-1.22 1.192
gulosus	3.82-4.58 4.153±.160	36.2-64.0 46.72±5.55	0.35-0.73 0.519±.115	1.08-2.26 1.547±.254	0.40-0.86 0.652±.096	0.94-1.05 0.966±.020	1.09-1.20 1.149±.026
thompsoni	3.87-5.50 4.659±.309	35.5-59.0 45.05±6.22	0.17-1.12 0.497±.182	0.71-1.35 1.014±.128	0.20-0.52 0.325±.057	1.02-1.11 1.053±.017	1.11-1.21 1.163±.024
trophonius	3.61-4.03 3.825±.131	29.5-37.3 32.95±2.21	0.36-0.58 0.431±.061	0.98-1.31 1.101±.118	0.32-0.44 0.380±.035	0.89-0.94 0.913±.018	1.15-1.23 1.175±.026
erebus	4.05-4.93 4.443±.225	42.5-65.4 51.27±6.64	0.13-0.62 0.322±.129	1.53-3.03 1.976±.330	0.54-0.83 0.661±.087	0.93-1.01 0.975±.023	1.11-1.21 1.150±.032
plutonis	3.80-4.39 4.072±.184	38.9-52.3 45.44±4.38	0.59-1.50 0.884±.284	1.32-1.69 1.578±.119	0.46-0.65 0.549±.069	0.98-1.02 1.002±.015	1.02-1.08 1.038±.020
torridus	3.43-3.99 3.717±.237	36.9-43.0 39.11±2.43	0.59-1.46 0.941±.282	1.39-1.62 1.524±.079	0.41-0.59 0.508±.056	0.98-1.02 0.999±.013	1.12-1.17 1.150±.016

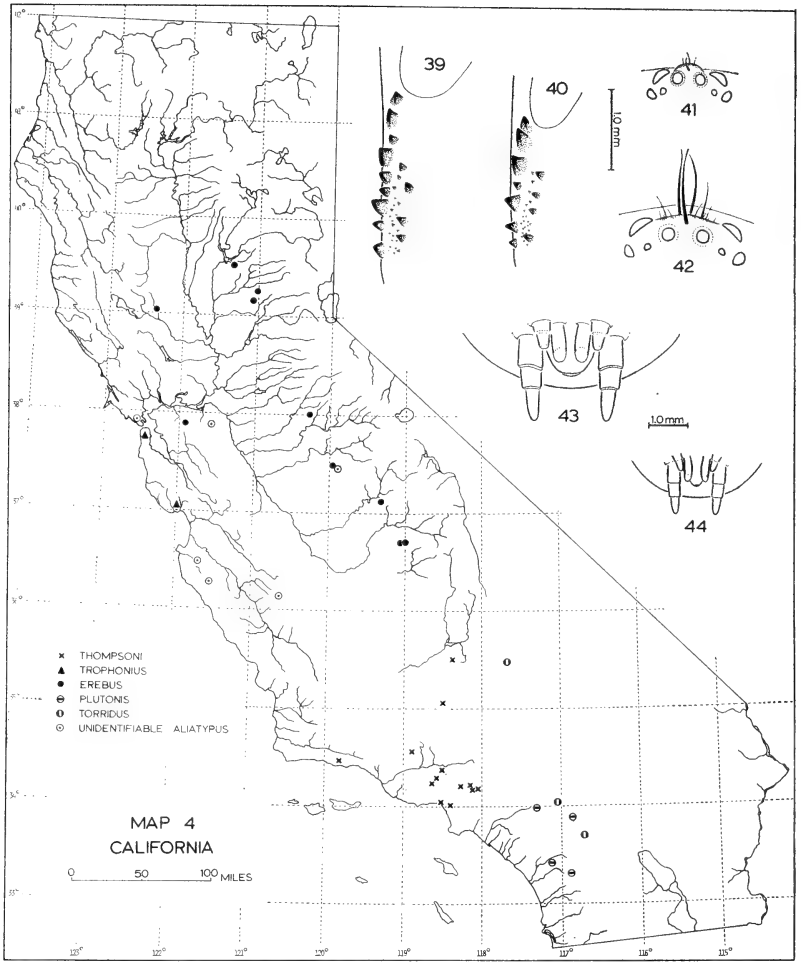
	SL/SW	SW/PSS	SW/PSL	PSL/PSS	AMD/AMS	IMS/CMT	IMS/PSS
californicus	1.15-1.33 1.240±.049	2.57-4.36 3.188±.350	6.52-11.03 9.011±1.105	0.23-0.63 0.363±.085	0.46-1.06 0.721±.147	0.39-2.67 0.928±.426	8.7-20.6 14.76±2.82
janus	1.21-1.36 1.283±.033	2.71-4.30 3.411±.439	6.19-10.94 8.378±1.121	0.25-0.67 0.419±.103	0.39-0.82 0.594±.103	0.32-2.44 1.339±.547	13.1-34.7 21.24±6.24
isolatus	1.13-1.24 1.173±.031	2.67-3.58 2.956±.263	8.29-16.16 11.191±2.473	0.18-0.43 0.278±.076	0.44-0.71 0.605±.076	0.68-2.09 1.204±.416	13.5-27.1 17.47±3.78
aquilonius	1.13-1.30 1.205±.042	2.28-3.39 2.705±.308	8.76-20.00 13.322±2.951	0.13-0.39 0.217±.073	0.50-0.83 0.709±.083	0.69-2.33 1.267±.377	10.8-22.9 16.63±2.72
gnomus	1.17-1.27 1.218	2.56-2.72 2.662	9.27-14.08 11.611	0.18-0.29 0.236	1.36-1.71 1.492	1.40-1.86 1.595	19.7-22.8 20.94
gulosus	1.02-1.23 1.157±.035	2.60-3.43 2.989±.185	7.05-13.67 9.444±1.226	0.24-0.43 0.322±.052	0.31-0.63 0.462±.084	0.44-1.43 0.821±.246	6.1-13.3 8.64±1.49
thompsoni	1.03-1.28 1.171±.068	6.60-18.39 9.488±2.151	3.31-5.73 4.510±.551	1.33-4.06 2.130±.522	0.39-1.33 0.666±.165	0.33-2.90 1.584±.622	33.3-116.6 57.60±15.81
trophonius	1.06-1.16 1.119±.028	3.61-5.12 4.235±.475	4.79-6.56 5.252±.582	0.55-1.07 0.820±.153	0.48-0.76 0.623±.089	0.86-1.38 1.138±0.153	18.7-26.1 21.58±2.29
erebus	1.09-1.24 1.156±.032	4.26-8.47 5.536±.850	3.81-5.27 4.551±.371	0.84-2.00 1.232±.259	0.29-0.68 0.438±.104	0.16-1.09 0.509±.243	11.1-24.4 15.60±3.71
plutonis	1.07-1.18 1.136±.037	5.09-6.09 5.641±.316	3.93-4.61 4.352±.241	1.19-1.41 1.298±.072	0.36-0.60 0.465±.072	0.91-3.25 1.662±.705	16.1-24.5 19.39±2.61
torridus	1.11-1.22 1.159±.034	4.37-5.38 4.717±.314	4.60-5.41 4.973±.376	0.81-1.05 0.953±.093	0.42-0.59 0.527±.054	1.00-3.25 1.898±.678	15.0-20.5 17.10±.2.19

TABLE 3. QUANTITATIVE CHARACTER VALUES FOR HOLOTYPE SPECIMENS OF *ALIATYPUS* SPECIES
(All measurements are in mm. *A. californicus* holotype is a penultimate male.)

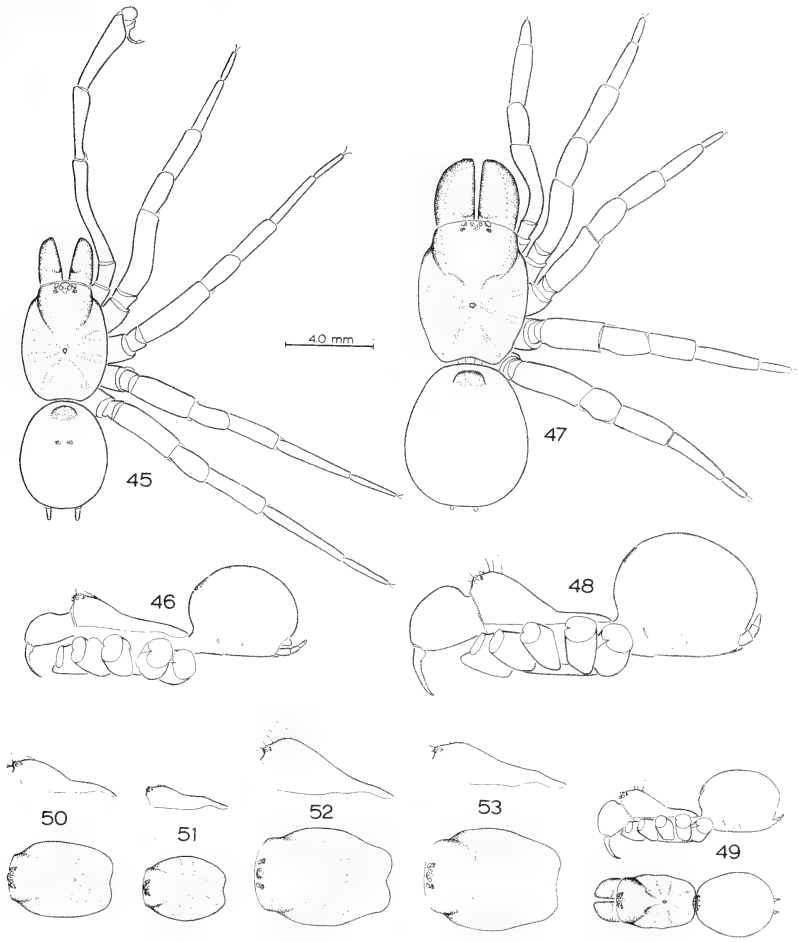
	californicus	*janus*	*isolatus*	*aquilonius*	*gnomus*	*gulosus*	*thompsoni*	*trophonius*	*erebus*	*plutonis*	*torridus*
CL	5.5	5.5	4.9	3.1	3.1	3.7	4.2	3.7	4.9	4.3	4.0
PCL	3.31	3.15	2.92	1.69	1.77	2.15	2.54	2.15	2.92	2.54	2.38
CW	4.16	4.31	4.08	2.46	2.54	3.04	3.46	2.84	3.73	3.46	3.07
IFL	4.00	5.15	4.85	3.19	2.92	3.73	5.08	2.77	3.69	4.08	3.54
ITL	2.38	3.15	3.00	1.92	1.96	2.38	3.04	1.65	2.19	2.38	2.07
IML	2.00	3.50	3.23	2.07	1.96	2.46	3.81	1.92	2.38	2.61	2.30
ITarL	1.08	1.73	1.57	1.07	1.07	1.61	1.84	1.15	1.42	1.50	1.27
PFL		5.42	5.31	3.23	3.07	4.15	4.77	2.65	3.77	4.61	3.73
PPL		2.92	3.00	2.15	1.84	2.50	3.07	1.69	2.42	3.00	2.15
PTL		3.81	3.77	2.27	2.23	3.58	3.19	1.92	2.77	3.38	2.84
PTX		2.84	2.77	1.61	1.61	1.61	2.38	1.38	2.00	2.54	1.84
PTT		0.94	0.90	0.49	0.53	0.64	0.85	0.81	1.12	0.81	0.75
PED		1.23	1.25	0.83	0.73	0.64	1.23	0.86	0.94	0.99	1.01
PCA		0.51	0.57	0.36	0.33	0.31	0.70	0.53	0.53	0.59	0.57
SL	3.38	3.31	2.84	1.69	1.77	2.15	2.30	2.00	2.84	2.46	2.30
SW	2.77	2.61	2.30	1.38	1.38	1.84	2.00	1.80	2.38	2.19	1.96
PSS	0.89	0.83	0.77	0.64	0.62	0.72	0.27	0.48	0.55	0.42	0.53
PSL	0.28	0.36	0.25	0.09	0.12	0.16	0.46	0.29	0.51	0.44	0.35
OQW	1.24	1.12	1.22	0.73	0.83	0.99	1.09	0.98	1.09	1.12	1.14
ALS	0.67	0.61	0.62	0.42	0.40	0.49	0.49	0.55	0.57	0.64	0.64
ALD	0.31	0.29	0.25	0.20	0.22	0.25	0.25	0.25	0.27	0.29	0.25
AMS	0.20	0.18	0.15	0.09	0.12	0.14	0.15	0.13	0.19	0.19	0.18
AMD	0.17	0.12	0.16	0.12	0.11	0.16	0.13	0.17	0.15	0.17	0.14
EGS		29	25	11	10	21	22	24	27	19	22



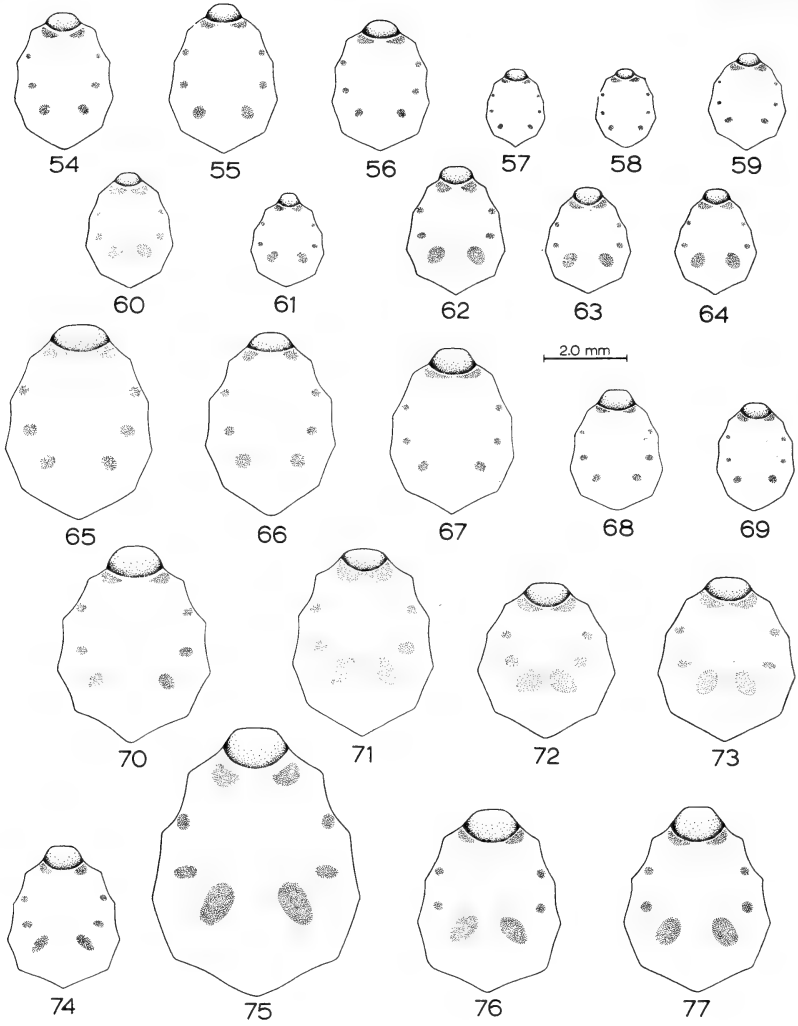
Maps 2-3. Distribution of *Aliatypus* species.



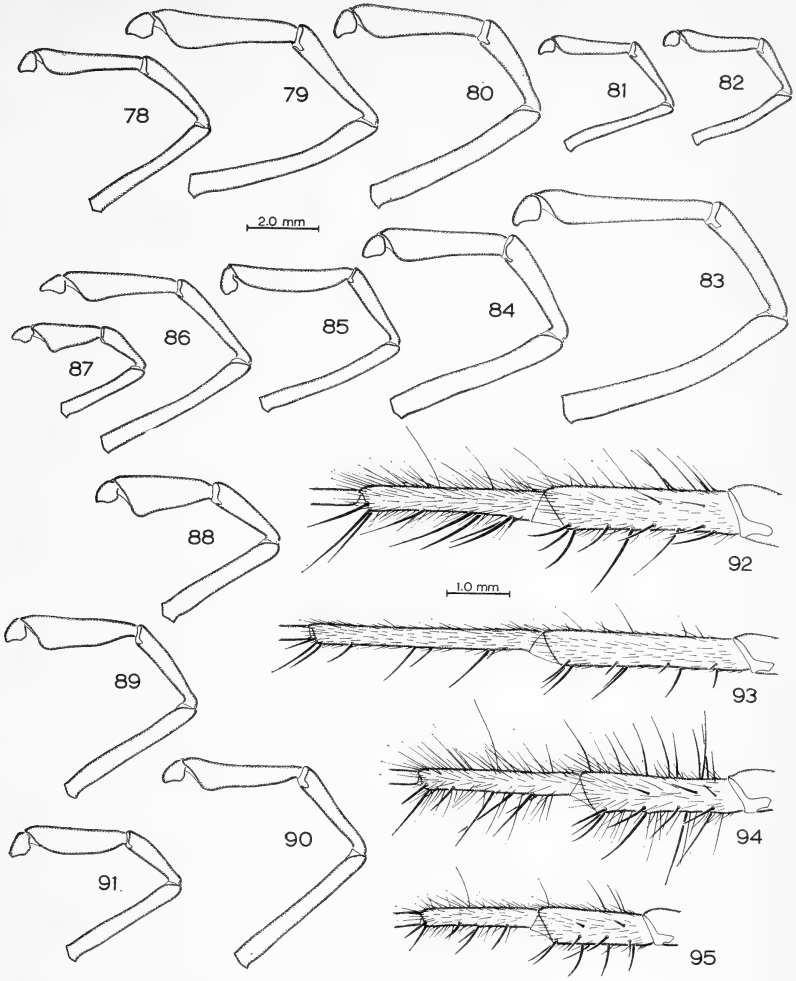
Map 4. Distribution of *Aliatypus* species. (Unidentifiable specimens are immatures and females which cannot be assigned to any recognized species.) Figures 39-40: Cheliceral teeth of *Aliatypus* females. (Ventral view of left chelicera.) 39: *A. californicus,* Soquel. 40: *A. thompsoni,* paratype. Figures 41-42: Eyes of *Aliatypus thompsoni* (Dorsal view with lateral border of carapace horizontal.) 41: male, holotype. 42: female, paratype. Figures 43-44: Spinnerets of *Aliatypus thompsoni.* (Ventral view.) 43: female, paratype. 44: male, paratype.



Figures 45-53: Whole body and carapace views of *Aliatypus*. 45-48: *A. californicus*. 45-46: male, Calaveras Reservoir. 47-48: female, Soquel. 49: *A. gnomus* female, paratype. 50-53: *A. thompsoni*. 50-51: males. 50: Placerita Canyon. 51: Henninger Flats. 52-53: females 52: Placerita Canyon. 53: Henninger Flats.



Figures 54-77: Sternum, labium, and sigilla of *Aliatypus* species. 54-64: males. 54: *A. californicus,* Alum Rock Park. 55: *A. janus,* holotype. 56: *A. isolatus,* paratype. 57: *A. aquilonius,* holotype. 58: *A. gnomus,* holotype. 59: *A. gulosus,* holotype. 60: *A. thompsoni,* paratype. 61: *A. trophonius,* holotype. 62: *A. erebus,* holotype. 63: *A. plutonis,* Banning. 64: *A. torridus,* holotype. 65-77: females. 65: *A. californicus,* Montebello Rd. 66: *A. janus,* paratype. 67: *A. isolatus,* paratype. 68: *A. aquilonius,* paratype. 69: *A. gnomus,* paratype. 70: *A. gulosus,* paratype. 71-73: *A. thompsoni.* 71: paratype. 72-73: Eaton Canyon. 74: *A. trophonius,* paratype. 75: *A. erebus,* Sonora. 76: *A. plutonis,* Banning. 77: *A. torridus,* paratype.



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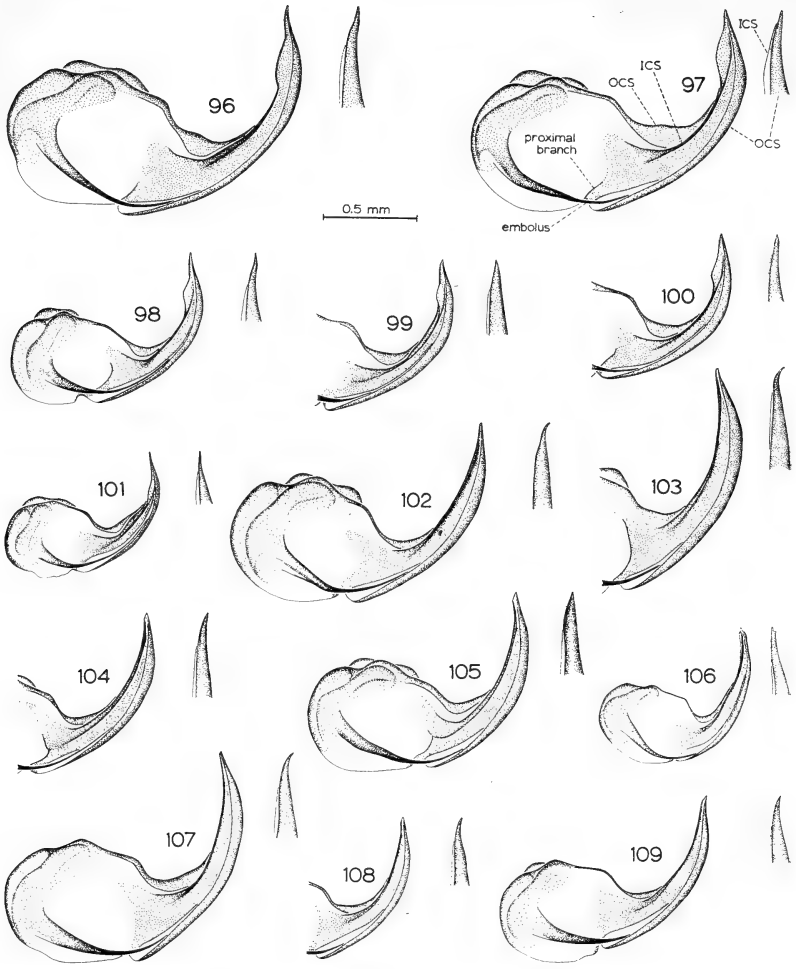

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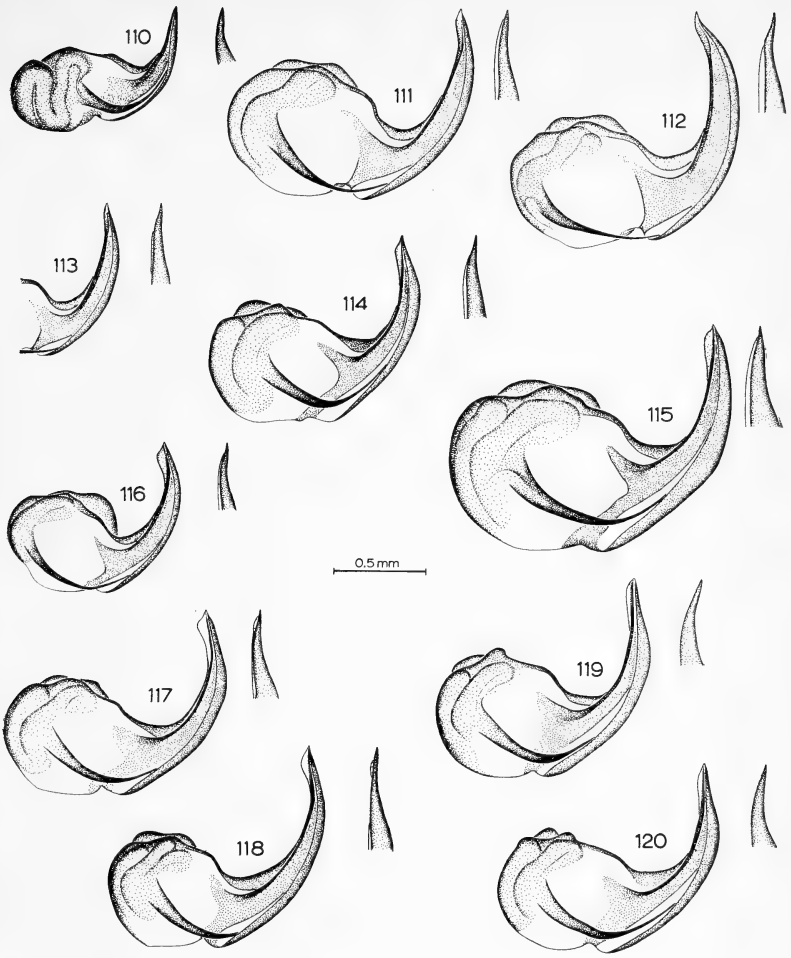

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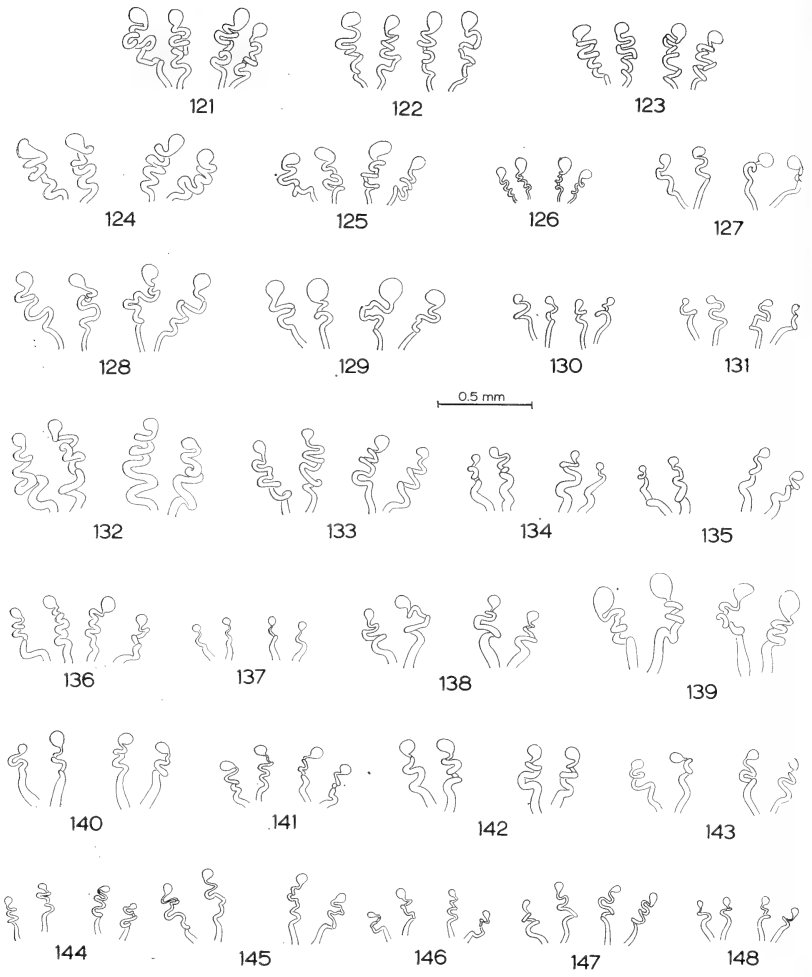

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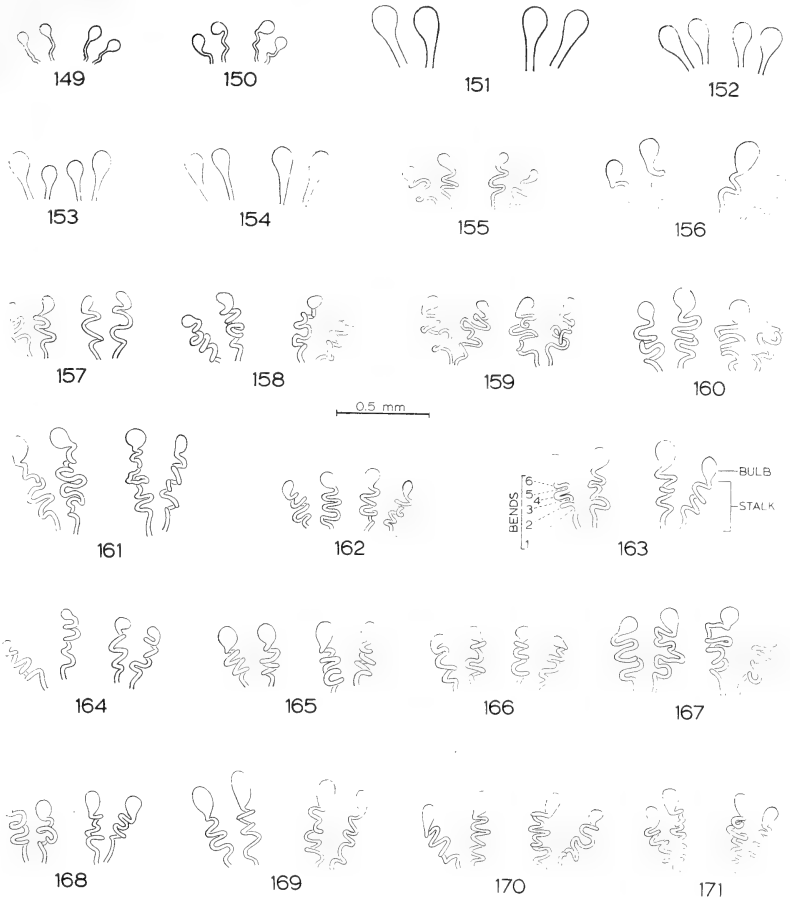
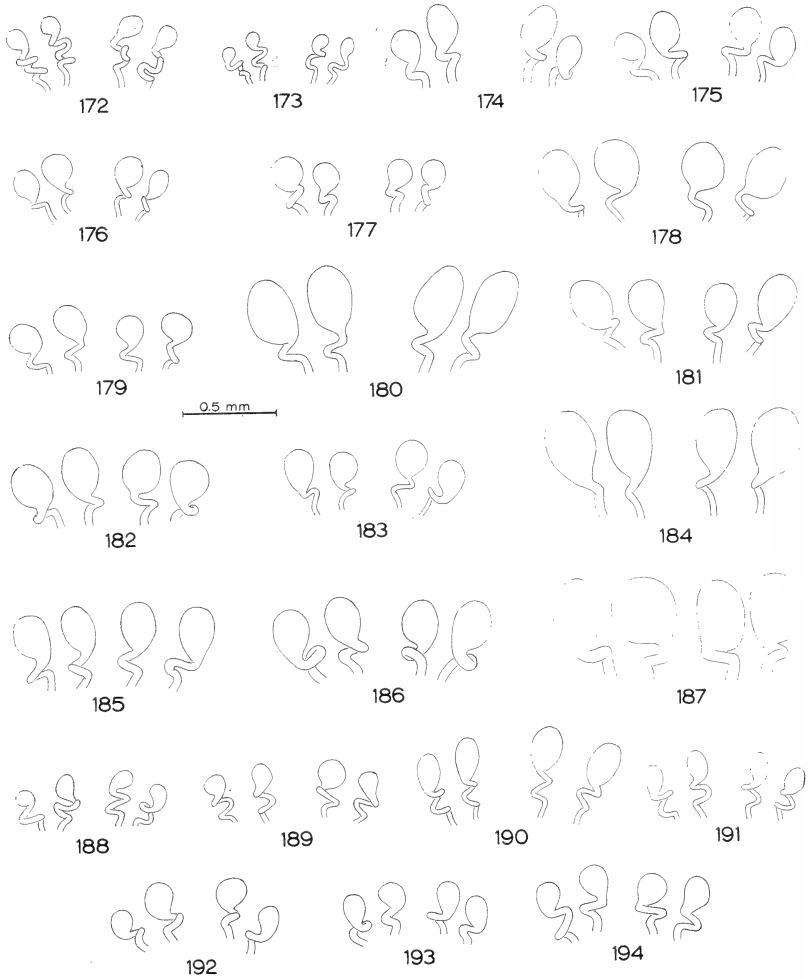


Figures 149-171: *Aliatypus* seminal receptacles. (Dorsal view.) 149-150: *A. gnomus* paratypes. 151-154: *A. gulosus*. 151: Eaton Canyon. 152: Sierra Madre. 153-154: paratypes. 155-171: *A. thompsoni*. 155: Kernville. 156-157: Tehachapi Mtns. 158: Santa Ynez. 159: Squaw Flats. 160-161: Placerita Canyon. 162: Baldwin Hills. 163: Limekiln Canyon. 164-166: paratypes. 167: Las Barras Canyon. 168: Henninger Flats. 169-170: Eaton Canyon. 171: Sierra Madre.



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A REVIEW OF THE *AGYRTES* (SILPHIDAE) OF NORTH AMERICA*

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Dr. John Lawrence and Dr. Roy Crowson pointed out to me that the type specimen of *Lendomus politus* Casey (placed in Mycetophagidae by Casey) seemed to be a silphid in the genus *Agyrtes*. This led me to study the Casey type and to review the species of *Agyrtes* of North America as the first part in a projected series of reviews of the silphid genera of North America.

The genus *Agyrtes* is Holarctic. Seven species are known and a key to them is given by Hlisnikovsky (1964). Of these, two species occur in and are limited to North America. The habits of the North American species are unknown, but the European species occur in forests under bark, in moss, and at rotting mushrooms.

Agyrtes longulus (LeConte)

Figures 1, 2, 8, 9, 10.

Necrophilus longulus LeConte, 1859: 282. Lectotype here designated as female in MCZ, LeConte colln. (no. 3148), bearing gold disc, seen. Type locality: Table Mountain, below San Francisco, California, by original designation.

Agyrtes longulus (LeC.). Horn, 1880:246. Hatch, 1957:8.

Lendomus politus Casey, 1924: 184. New Synonym. Holotype male in USNM, Casey colln. (no. 37497), seen. Type locality; Anticosti Island, Quebec, Canada. No other type data.

Diagnosis. Antennal club composed of four segments, first three of club with rings of dense pubescense on inside apical margin, third antennal segment appreciably longer than the second. Prothorax conspicuously wider than long, less narrowed towards the front, posterior angles distinct. Aedeagus in side view with pronounced bend (fig. 10), paramere an elongated spatula (fig. 9).

Distribution. The species ranges from southern California northwards through the coastal mountains to British Columbia and southern Alaska, and inland to Idaho. In addition to the type I have seen the following material:

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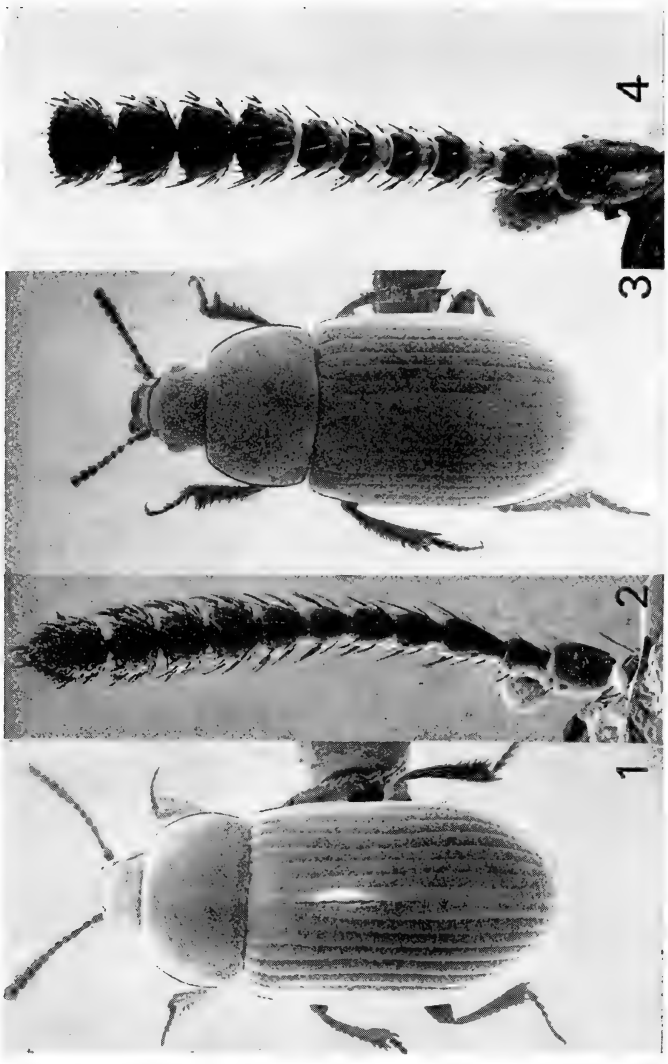


Figures 1-4. 1. *Agyrtes longulus*. 2. Antenna of *A. longulus*. 3. *A. similis* 4. Antenna of *A. similis*, segment eleven missing.

Canada. British Columbia. Creston. 15-xi-31, G. Stace Smith (abbreviated subsequently as GSS), 1 (CNCI); 29-ii-32, GSS, 1 (CAS): 11-xi-32, GSS, 1 under wood at 2000′ (CAS); 10-xi-33, GSS, 1 on ground, 2000′ (MCZ); 29-xi-33, GSS, 1 in flood debris at 1750′ (MCZ); 1-xi-45, GSS, 1 (MCZ); 21-xi-50, GSS, 3 on snow (CAS); 24-xi-50, GSS, 1 on snow (CAS); 27-xi-50, GSS, 23 on snow (CAS); 10-xii-50, GSS, 1 on snow (CAS); 1952, GSS, 4 (FMNH); 26-iii-56, GSS, 1 (CNCI); 18-iv-56, GSS, 1 (CNCI). Queen Charlotte Islands. Massett, 10 (USNM); no locality, 5 (CAS, CNCI, USNM). Salmon Arm, 11-iv-28, HB Leech, 1 (CNCI); 12-iv-35, H. Leech, 1 (MCZ); 21-xii-35, SH & O Leech, 1 on snow (CAS). Terrace, viii-1927, ME Hippsley, 1 (MCZ); ME Clark, no other data, 1 (MCZ). Vancouver, 28-i-31, HB Leech, 2 (CAS, CNCI); 26-iii-33, HB Leech, 1 flying, (Fall colln. MCZ); no other data, 1 (LeConte colln., MCZ).

United States. Alaska. Sitka, 5 (USNM). California, Alameda County, Berkeley, 22-ii-20, JO Martin, 3 (CAS). Glenn County, Elk Creek, 17-iv-13, R Hopping, 1 on *Pinus ponderosa* (CAS). Marin County, Mill Valley, 22-ii-26, Van Duzee, 1 (CAS); 8-x-51, RE Leech, 1 at light (CAS); 9-i-56, HB Leech, 1 (CAS). Mt. Tamalpais, 23-v-09, Van Dyke, 1 (CAS). Taylorville, 28-xii-19, JO Martin, 1 (CAS). Monterrey County, Carmel, 27-xii-14, 1 (CAS). Plumas County, 2 (USNM). San Francisco County, San Francisco, 8-i-11, Van Dyke, 1 (CAS). Santa Clara County, no other data, 1 (CAS). Sonoma County, Eldridge, 17-xii-10, Van Dyke, 2 (CAS); southern Sonoma County, 9-xii-10, Van Dyke, 2 (CAS); 11-xii-10, 1 (CAS); 14-xii-10, Van Dyke, 3 (CAS). 29-i-11, Van Dyke, 3 (CAS). Oregon. No other data, 1 (USNM). Clackamas County, Colton, iv-35, ES Ross, 1 (CAS); Yamhill County, 2-iii-34, ES Ross, 1 (CAS). Washington. King County, Seattle, 3-v-14, 2 (Fall colln., MCZ); 28-ii-98, 1 (CAS); no other data, 3 (CAS). Thurston County, Olympia, no other data, 1 (Fall colln., MCZ).

Hatch (1957) also mentions that the species occurs in northern Idaho.

Biology. Virtually nothing is known of the habits of the species or of its life cycle. The seasonality data show that it is most active in the winter months. The species has been taken most often on snow but also in flood debris, and under chips of live oak. It is presumably associated with forested habitats.

Notes on synonymy. The type of *Lendomus politus* Casey was examined and dissected. It was found to be identical, within reason-

able limits of variation in the shape of the aedeagus, with *Agyrtes longulus*. Since a number of beetles in eastern Canada have been introduced from Europe (Lindroth, 1957) there was the possibility that the *Agyrtes* of Casey might be a species introduced from Europe. It was compared with the European *A. castaneus* (F.) and the aedeagus drawings of Hlisnikovsky (1964) and was found to be distinctly different.

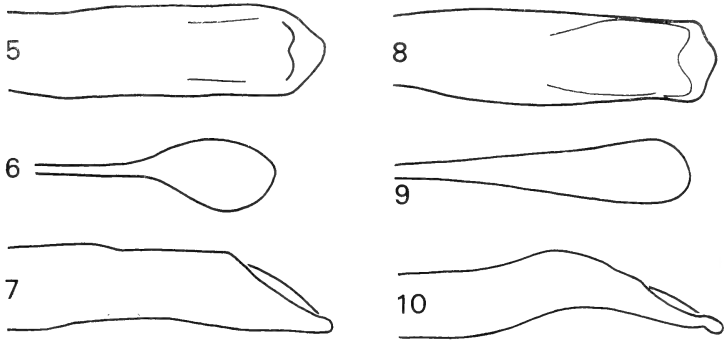
Since Casey's specimen is the only *Agyrtes* known from eastern North America, I think that an error was made in the labeling of Casey's *Agyrtes,* and we may continue to believe that the genus *Agyrtes* and the species *A. longulus* occur only in the coastal and interior mountains of western North America.

Agyrtes similis Fall

Figures 3, 4, 5, 6, 7.

Agyrtes similis Fall, 1937; 29. Holotype male in MCZ, Fall colln. (no. 24015), seen. Type locality: Pasadena, California.

Diagnosis. Antennal club composed of five segments, first four of club with rings of dense pubescense on inside apical margins, third antennal segment only a little longer than the second. Prothorax wider than long but more elongate and more gradually narrowed toward the front, posterior angles rounded. Aedeagus in side view relatively straight (fig. 7), paramere a rounded spatula (fig. 6).



Figures 5-10. 5. *A. similis* aedeagus, dorsum, Pasadena, California. 6. *A. similis* paramere, setae omitted. 7. *A. similis* aedeagus, lateral view. 8. *A. longulus* aedeagus, dorsum, Mill Valley, Marin Co., California. 9. *A. longulus* paramere, setae omitted. 10. *A. longulus* aedeagus, lateral view.

Distribution. The species is known only from the coastal ranges of central and southern California. In addition to the type I have seen the following specimens:

California. Alameda County, Alameda, 1-iv-90, 1 (Koebele colln., CAS). Los Angeles County. Pasadena, Jan., 1; Feb., 1; Mar., 1; (Fenyes Colln., CAS). Pomona, mountains, 15-xi-96, 1 (Fall colln., MCZ). "Cala," no other data, 2 (Horn colln. in MCZ).

Biology. Nothing is known of the habits or life cycle of this beetle. The collection records show that it is active only in the winter months. It is presumably associated with forested habitats.

Notes. There is a remarkable similarity in the dorsal view of the aedeagus and of the paramere of *Agyrtes bicolor* Lap. of central Europe (as illustrated by Hlisnikovsky, 1964) and of *A. similis,* but other characters in the key of Hlisnikovsky seem to separate the species. The aedeagus of *A. bicolor* in side view is not illustrated. I have not studied material of *A. bicolor,* although I have seen the Hlisnikovsky collection in Prague.

Acknowledgements

I wish to thank the following for having made available for study material in the collections under their care: M. J. Campbell, Canadian National Collection of Insects, Ottawa (CNCI); H. Dybas, Field Museum of Natural History, Chicago (FMNH); J. M. Kingsolver, U. S. National Museum, Systematic Entomology Laboratory (USNM). J. F. Lawrence, Museum Comparative Zoology, Harvard University (MCZ); H. B. Leech, California Academy of Sciences, San Francisco (CAS). H. F. Howden and J. F. Lawrence are thanked for reviewing the manuscript. L. E. C. Ling of Carleton University took the SEM photographs.

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APPLICATION OF THE TRANSMISSION ELECTRON MICROSCOPE TO THE EXAMINATION OF SPIDER EXUVIAE AND SILK*

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In recent years the scanning electron microscope (SEM) has been used fruitfully to study the fine structure of many arthropods, including spiders. The advantage of the SEM lies in the simple method of preparation — no embedding and sectioning has to be done — and its large depth of focus, which yields almost three-dimensional views of surface structures. Drawbacks of the SEM are a limited resolution (150-200 Å) and, as well, lack of availability to most researchers. The transmission electron microscope (TEM) has a much better resolution (< 10Å) than the SEM, but requires objects of less than 0.1-0.2 μ thickness to allow penetration of the electron beam.

It was found that by simply mounting parts of spider exuviae (preferably of early instars) on Formvar-coated copper grids, details of hairs and claws can be seen with the TEM. If a leg tip of an exuvia is placed on a water droplet on the Formvar membrane, it will firmly adhere to the membrane after the water has evaporated. The preparation can then be viewed immediately in the TEM. Better stability and more contrast may be achieved by shadowing the specimen at an angle of 40-50° with a metal (e.g. copper). The very delicate scopula hairs (Fig. 1-4) are especially well-suited for examination with the TEM, but other hairs and bristles can also be easily surveyed and classified. For instance, the open tip of chemosensitive hairs (Foelix, 1970) is convincingly demonstrated with the TEM (Fig. 5).

Spider silk, especially the extremely fine threads of cribellate silk (Fig. 6), has been studied with the TEM before (Lehmensick and Kullman, 1957; Friedrich and Langer, 1969). It should be emphasized here that shadowing with copper yields much more stable preparations. Ecribellate silk is often too thick (1-2 μ) to be examined with the TEM, but accurate measurements of the diameter of various threads can be performed (Fig. 7). The substructure of the sticky

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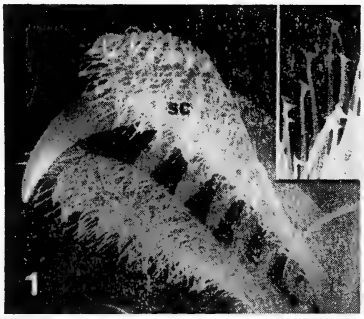
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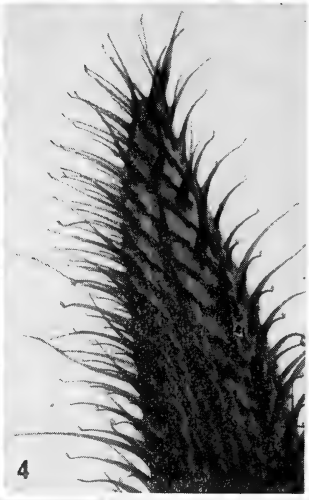
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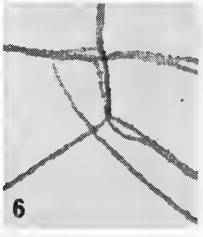
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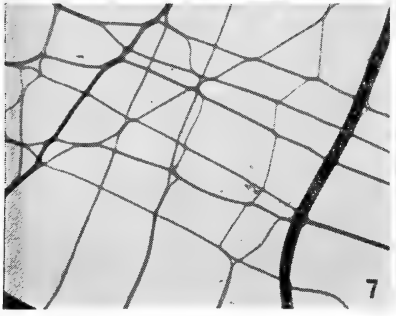
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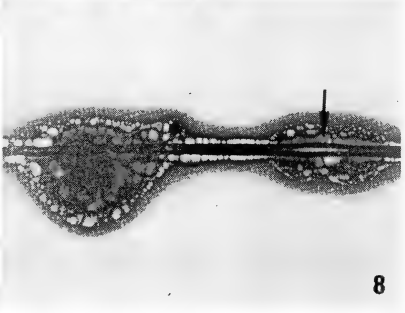
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spiral of orb weavers, however, can be revealed: The glue substance partially disintegrates under the electron beam and the two axial threads become clearly visible (Fig. 8).

It is hoped that this simple technique will be usefully applied to morphological as well as taxonomical problems.

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Explanation of Figures on Opposite Page

Fig. 1. Leg tip of *Philodromus aureolus* (nymph 2) as seen with the SEM. Scopula hairs (sc) surround the combed main claw. 1400 ×. Inset: Scopula hairs bear fine extensions with terminal 'end-feet'. 4200 ×. (Courtesy of Dr. W. Gnatzy). Fig. 2. The 'end-feet' of a scopula hair of *Philodromus* seen with the TEM. 7000 ×. Fig. 3. Leg tip of *Alopecosa accentuata* (nymph 2) showing one main claw (M), chemosensitive hairs (c), mechanosensitive hairs (m) and a scopulate hair (sc). TEM, 630 ×. Fig. 4. Scopulate hair of *Micrommata virescens*. Note the small end-feet. TEM, 4200 ×. Fig. 5. Tip of a chemosensitive hair of *Philodromus*. Note the terminal pore opening (arrow). TEM, 12600 ×. Fig. 6. Cribellate silk from *Amaurobius ferox*. The diameter of single threads is less than 200 Å. Little knobs become accentuated by the metal shadowing. TEM, 28000 ×. Fig. 7. Ecribellate silk from the silken cell of a *Heliophanus*. A mesh-work of fine fibers (0.1 μ) underlies several stronger fibers (0.5 μ). TEM, 2800 ×, unshadowed. Fig. 8. Sticky spiral thread from *Zygiella x-notata*. The peripheral glue substance has precipitated around the double axial threads (arrow). TEM, 630 ×.

PLASTRAL RESPIRATORY DEVICES IN ADULT *CRYPHOCRICOS* (NAUCORIDAE: HETEROPTERA)*

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Introduction

Adult *Cryphocricos* live in very rapid, well-aerated streams, under stones and gravel at depths of from 6 to 24 inches (Fritz Plaumann, personal communication; John Polhemus, personal communication; Randall Schuh, personal communication). Under these conditions it would be difficult for these insects to come to the water surface for atmospheric air, as do "slow-water" Naucoridae and most other aquatic Heteroptera, and neither Polhemus (personal communication) nor Schuh (personal communication) have observed them to do so.

Even if it were possible for *Cryphocricos* to obtain atmospheric air, the insects lack a means of storing large amounts of it for underwater respiration. Aquatic Heteroptera with "air-bubble" respiration carry much atmospheric air under their long forewings and trapped by long hairs on the ventral surfaces of their bodies. Long-winged *Cryphocricos,* however, are very rare. Most individuals lack hindwings and have forewings which reach only to the third abdominal segment. The reduced subalar space on the pterothorax is too small to hold any appreciable amount of air (Parsons 1974). Thorpe (1950) concluded, from examination of a dried specimen of *Cryphocricos* sp., that it is "a bubble-carrier rather than a true plastron insect" and has "a substantial air film". Polhemus, however, examined *C. hungerfordi* in the field and observed no such air layer except on the six pairs of small ventral abdominal sense organs (Polhemus, personal communication). Parsons (1974) observed a very thin air layer on the ventral surfaces of the thorax and abdomen in formalin-preserved *C. barozzii,* but this layer is visible only under the stereoscopic microscope and is usually hidden by the debris which covers the insect.

Young's (1944) suggestion that *Cheirochela* (Naucoridae) survives by cutaneous respiration appears highly dubious, and it is unlikely that *Cryphocricos* uses this method to any great extent. The

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exoskeleton is quite thick, and the relatively large size of the insect (*C. hungerfordi* is 8.5-9.5 mm long; *C. barozzii* is 10-13 mm long) produces an unfavorable ratio of volume to surface area.

Among the aquatic Heteroptera, true plastral respiration has thus far been experimentally demonstrated only in *Aphelocheirus* (Thorpe and Crisp 1947a, 1947b; Thorpe 1950). Whether this insect is a naucorid (Usinger 1956) or represents a separate family, the Aphelocheiridae (Parsons 1969) is debatable. *Aphelocheirus* possesses a very thin, permanent air layer, or "plastron", which is retained by short, densely-packed hairs on most of the dorsal and ventral surfaces of the body. The plastron is exposed to the water and acts as a gill, obtaining enough dissolved oxygen from the water to make the insect independent of atmospheric oxygen (Thorpe and Crisp 1947a; Thorpe 1950). *Cryphocricos* and *Aphelocheirus* share such morphological similarities as reduced forewings, vestigial hindwings, lack of a large air store, and paired abdominal pressure receptors of a type not yet reported in any other Heteroptera (*Aphelocheirus,* Thorpe and Crisp 1947c, Larsén 1955; *Cryphocricos,* Thorpe 1950, Parsons 1974). These similarities suggest that *Cryphocricos,* like *Aphelocheirus,* has a plastral type of respiration. Hinton (1969a, p. 198) has remarked that "Por ejemplo, entre insectos adultos hay por lo menos cuatro orígenes independientes de respiración de plastrón dentro de la familia Naucoridae: *Aphelocheirus, Cryphocricos, Heleocoris,* e *Idiocarus*". He included a photomicrograph of thoracic plastral hairs in *Heleocoris* but did not further elaborate on his statement.

Although the presence of plastral respiration would be best demonstrated by both morphological and physiological studies, live specimens of *Cryphocricos* were not available for experimentation. Our investigation, like Hinton's (1969b) study on aquatic beetles, was therefore confined to morphology. Its purposes were (1) to discover whether the exposed surfaces of the body possess hydrofuge devices which might retain a thin plastral air layer, and (2) briefly to compare any such structures with those of other insects in which plastral respiration is believed to occur.

Materials and Methods

Species used:

Cryphocricos barozzii Signoret (preserved in formalin; collected in Brazil by F. Plaumann; two specimens)

C. hungerfordi Usinger (preserved in alcohol; collected in Mexico by J. T. Polhemus; one specimen)

Aphelocheirus aestivalis Fabricius (preserved in Bouin's fluid; collected in England by D. T. Crisp; two specimens)

The specimens were first dissected in 80% alcohol under a stereoscopic microscope. They were cut midsagittally with a razor blade and the ventral and dorsal surfaces of one or both halves were separated along the lateral edge. On one specimen of *Aphelocheirus* a small section of the metathoracic episternum was removed so that the cut edge could be examined. A major obstacle was the presence of large amounts of silt and other debris on the external surfaces of all three species. Treatment with weak solutions of either potassium hydroxide or Sparkleen detergent failed to remove it. Somewhat better results were obtained by scraping small areas with watchmaker's forceps.

The specimens were then mounted with double-sided tape on aluminum stubs, freeze-dried, and coated, in an Edwards vacuum evaporator, Model 4, with a layer of gold which was approximately 200-400 Å thick. They were examined in a Cambridge Stereoscan, Model 2A, and photographed with a Singer camera, using Ilford 120 roll film.

Observations

Ventral Surface

(1) *Plastral Hairs*

In both species of *Cryphocricos* most of the ventral surface is covered with densely-packed hairs (Fig. 3). They occur on the pro-

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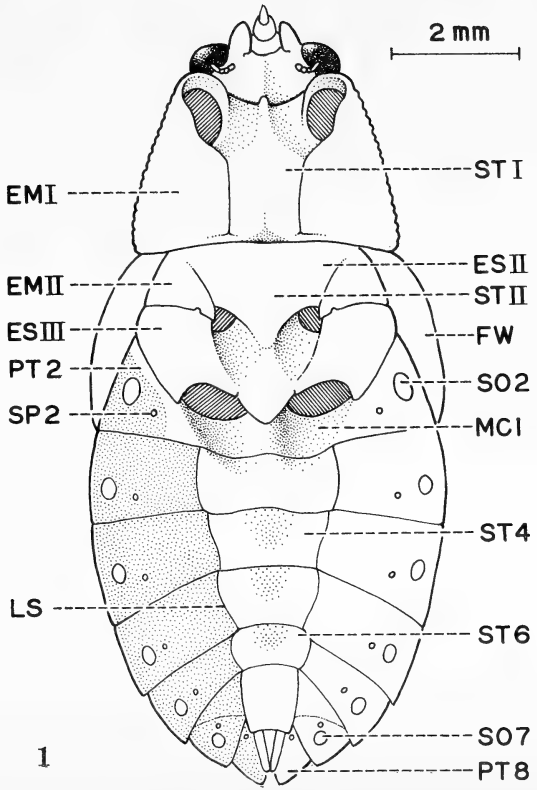
Fig. 1. *Cryphocricos barozzii;* ventral view, legs removed. Stippling on fourth through sixth abdominal sternites indicates area of microtrichia (Fig. 11); stippling on ventral abdominal paratergites, left side of figure, indicates area of short leaf-like setae (Figs. 6-8). Longer leaf-like setae occur on the six pairs of abdominal sense organs. Most of the ventral surface is covered with plastral hairs (Figs. 3, 4).

Abbreviations: EM, epimeron; ES, episternum; FW, forewing; LS, longitudinal sulcus; MCI, metacoxal indentation on abdomen; PT, ventral abdominal paratergite; SO, abdominal sense organ; SP, abdominal spiracle; ST, sternite. Arabic numerals indicate abdominal segments; Roman numerals indicate thoracic segments.

Fig. 2. *Cryphocricos barozzii;* dorsal view, right forewing removed, revealing smooth subalar surfaces on right side (even stippling). Other surfaces are roughened. For distribution of plastral hairs, see text.

Abbreviations: TI, TII, TIII, thoracic terga; T1, T2, T3, abdominal terga.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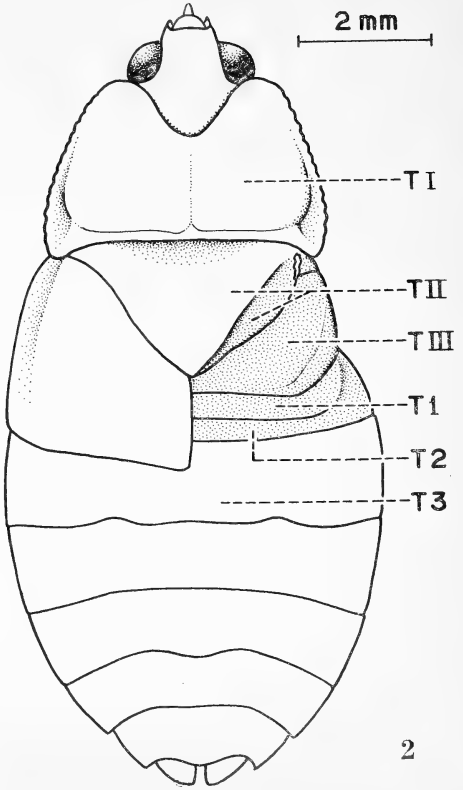
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thoracic epimeron and sternum (Fig. 1, EM I, ST I), the mesothoracic epimeron, episternum, and sternum (EM II, ES II, ST II), the metathoracic episternum (ES III), and all seven ventral abdominal paratergites (PT 2-PT 8). They also cover all of the third and seventh abdominal sternites and all but the anteromedial portions of the fourth through sixth sternites (ST 4-ST 6).

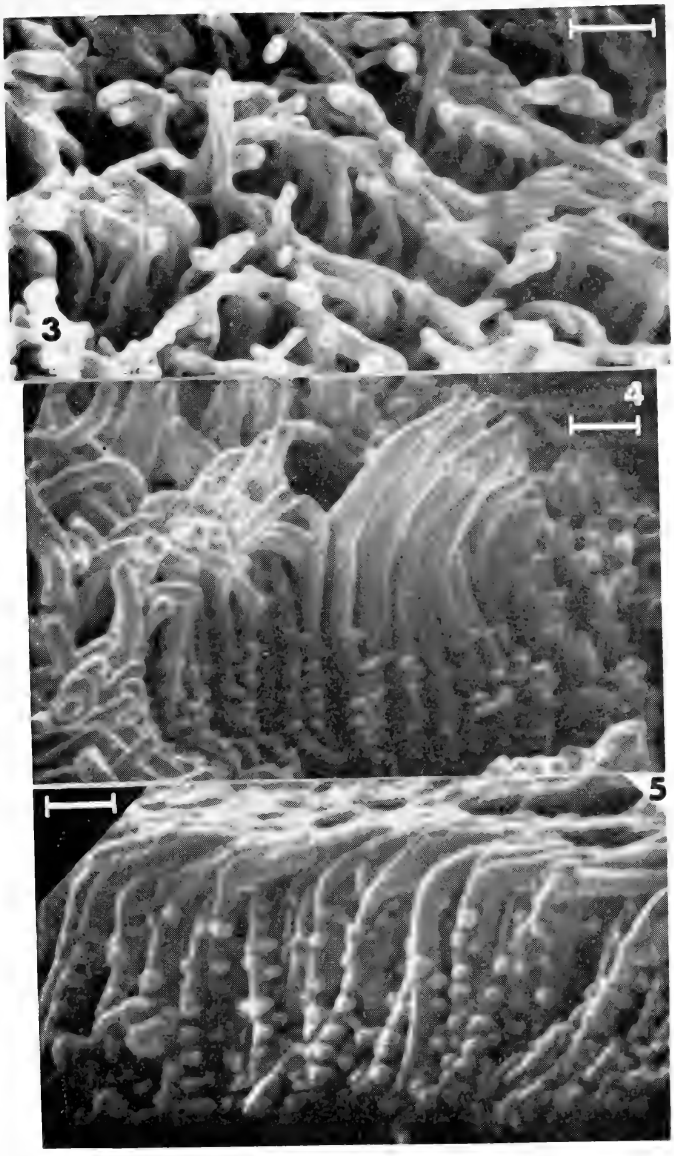
The close spacing of the hairs makes it difficult to see their bases and to measure their length. Their visible portions are at least 6 μm long and from 0.25 to 0.45 μm in diameter on the thorax and paratergites (Fig. 4). They are considerably shorter and wider on the abdominal sternites; on a sagittal cut through the fifth sternite, where the entire length of a few hairs was visible, they were only 2.7 μm long but 0.65 μm in diameter.

Comparison of the thoracic and paratergal hairs with the plastral hairs of *Aphelocheirus* (Fig. 5) shows similarities which strongly suggest that those of *Cryphocricos* (Fig. 4) are also plastral devices. The most striking similarities are (1) the presence of small nodules on the basal portions of the hairs, (2) the densely-packed arrangement of these hairs, and (3) the posterior bending of their apical portions, which lack nodules. Using the light microscope and transmission electron microscope, Thorpe and Crisp (1947a) observed the bending of the hairs in *Aphelocheirus* but did not see the nodules. The bending appears to be more pronounced in both specimens of *Aphelocheirus* than in the three specimens of *Cryphocricos*. In both genera the hairs tend to adhere to each other in clumps, making the direction of the bending difficult to detect in surface view (Fig. 3); the clumping is probably an artifact.

Fig. 3. *Cryphocricos barozzii;* surface view of apical parts of plastral hairs on metathoracic episternum. More basal parts of hairs, with nodules, visible at lower left. Clumping of tips is probably an artifact. Left = posterior, right = anterior. Scale line = 2 μm.

Fig. 4. *C. barozzii;* clump of plastral hairs on fifth ventral abdominal paratergite. Leaf-like setae, which concealed these hairs, were scraped off during preparation of specimen. Bases of hairs were concealed by tips of surrounding hairs. Note posterior (to right) bending of apices and presence of nodules on proximal parts of hairs. Scale line = 1 μm.

Fig. 5. *Aphelocheirus aestivalis;* cut edge of metathoracic episternum, showing full length of plastral hairs. Note posterior (to right) bending of apices and presence of basal nodules. Scale line = 1 μm.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The thoracic plastral hairs of *Aphelocheirus* are approximately 5-6 μm in length, as Thorpe (1950) also noted. They are thus somewhat shorter than those of *Cryphocricos,* but appear to be comparable to the latter in diameter. Their bases are somewhat thicker (approximately 0.4 μm) than their tips (approximately 0.3-0.35 μm). In both genera adjacent hairs seem to lie very close to each other. The nodules may help to hold them apart, allowing room for air to circulate between them. Also, because of the thickness of the gold coating (0.02-0.04 μm), the hairs probably appear, under the scanning electron microscope, somewhat thicker, and the intervening spaces smaller, than they actually are. By means of the light and transmission electron microscopes, Thorpe and Crisp (1947a) estimated the space between adjacent hairs on the abdominal sternites of *Aphelocheirus* to be approximately twice as great (0.4 μm) as the diameter of the tip of a single hair (0.18-0.25 μm). The discrepancy between their observations and ours may be due, in part, to the different techniques employed. It is also possible that the hairs are less densely packed on the abdominal sternites than on the thorax of *Aphelocheirus.*

The hairs of both *Cryphocricos* and *Aphelocheirus* are much shorter, narrower, and more densely packed than those which cover the ventral surface of the abdomen of *Pelocoris femoratus,* a "slow-water" naucorid with air-bubble respiration (Parsons 1974). A brief observation of one specimen of *Pelocoris* revealed that the hairs on the second abdominal paratergite lack basal nodules and are 30-40 μm long, 2-3 μm wide at the base, and approximately 10 μm apart.

(2) *Leaf-like Setae*

Leaf-like setae occur on the ventral paratergites of the abdomen (Fig. 1, light stippling lateral to LS). They extend all the way to the lateral edge of the body on the second abdominal paratergite, and nearly to the lateral edge on the more posterior paratergites. On the second paratergite (PT 2) a narrow anteromedial strip adjoining the metathoracic episternum (ES III) and the metacoxal indentation (MCI) lacks leaf-like setae (Fig. 6). This "nonfoliated" region is larger in *Cryphocricos hungerfordi* than in *C. barozzii.* The second abdominal spiracle (Fig. 1, SP 2) and sense organ (SO 2), like those of the other abdominal segments, lie in the "foliated" region.

In *C. barozzii* the flattened setae are widest (8-20 μm) near their bases and are 20-40 μm long. In *C. hungerfordi,* a smaller insect, they are approximately 75% this size. They appear to be socketed (Fig. 8) and are arranged somewhat like shingles, in closely packed,

Fig. 6. *Cryphocricos barozzii*: portions of left metathoracic episternum (upper left) and second ventral abdominal paratergite, showing arrangement of leaf-like setae on latter. Note absence of leaf-like setae on portion of paratergite immediately posterolateral to episternum. Top = anterior, bottom = posterior. Scale line = 50 μm. FIG. 7. *C. barozzii*; several leaf-like setae on third ventral abdominal paratergite. (Overlapping arrangement largely conceals underlying plastral hairs, which are visible at right. Scale line = 5μm.

somewhat irregular rows, each row overlapping the one posterior to it (Figs. 6, 7). The tapered tip of each seta points posteriorly and somewhat laterally on the body except in the spiracular regions, where those immediately lateral to the spiracles point posteromedially. On the eighth paratergite the setae are fewer and farther apart and do not overlap.

Under the stereoscopic microscope the ventral paratergites, unlike the "nonfoliated" regions of the body, have a faintly golden sheen. The sheen is visible when specimens are immersed in alcohol, which would remove any adherent air layer. It is probably the result of light diffraction by the fine longitudinal ridges on the ventral surfaces of the flattened setae (Figs. 7, 8).

In their shape and overlapping arrangement the setae resemble the plastral devices of *Phytobius* (Coleoptera; Thorpe and Crisp 1949). Unlike the latter, however, they do not bear plastral hairs on their external surfaces. The plastral hairs arise from the exoskeletal surface beneath the leaf-like setae and are largely concealed by them (Fig. 7) but were clearly visible in regions where the setae had been scraped off with watchmaker's forceps (Fig. 4). Although the setae do not completely cover the ventral abdominal spiracles they overlap so much of their margins that we could not observe spiracular structure or determine whether or not they possess radiating "rosettes" similar to those of the second through seventh abdominal spiracles of *Aphelocheirus* (Thorpe and Crisp 1947a).

The second through seventh abdominal sense organs (Fig. 1, SO 2-SO 7) are composed of leaf-like setae which are two to three times longer than those covering the rest of each paratergite (Fig. 9). Most of these elongated setae project more laterally than the shorter ones, and have blunter tips and more pronounced longitudinal ridges

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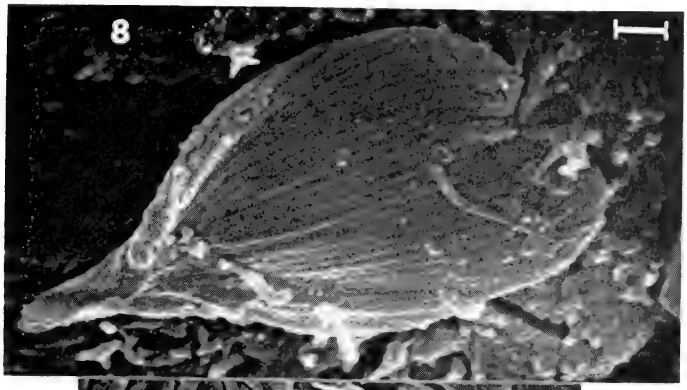
Fig. 8. *Cryphocricos hungerfordi;* detail of one leaf-like seta on fifth ventral abdominal paratergite. Note longitudinal ridges and tapering tip, which points posterolaterally (lower left). Surrounding setae were rubbed off, revealing tips of underlying plastral hairs and apparently socketed base of seta. Scale line = 2 μm.

Fig. 9. *C. barozzii;* sense organ on third ventral abdominal paratergite Sense organ is composed of elongated leaf-like setae. Tips of shorter leaf-like setae, covering rest of paratergite, are visible at bottom and upper left of figure. Right = lateral, bottom = posterior. Scale line = 30 μm.

Fig. 10. *C. barozzii;* detail of Fig. 9, showing longitudinal ridges on elongated leaf-like setae. Scale line = 2 μm.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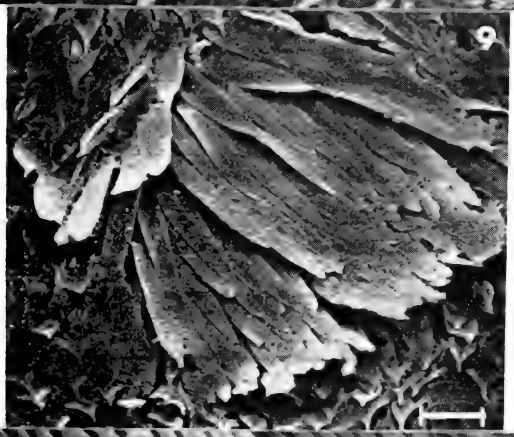
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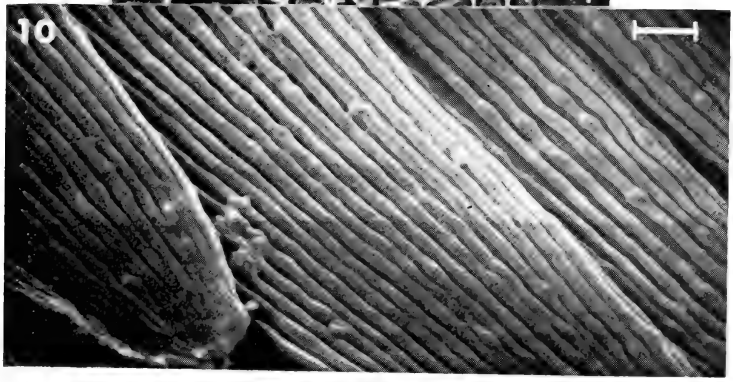
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(Fig. 10). A considerable quantity of air is trapped among these overlapping, elongated setae. On living specimens the sense organs are the only parts of the body on which air can be seen with the naked eye (Polhemus, personal communication), and the air on these regions is easily seen with the stereoscopic microscope.

In *Aphelocheirus* similar sense organs, which are probably pressure receptors, occur only on the second abdominal segment (Thorpe and Crisp 1947c). Like those of *Cryphocricos* they are composed of flattened, elongated setae, approximately 75 μm long, which point posterolaterally and overlap each other. The setae appear to be longitudinally ridged, although this could not be determined with certainty because of the large amount of debris which covered them. Leaf-like setae were not observed on any other region of the body of *Aphelocheirus*.

(3) *Microtrichia*

On the anteriormost portions of the fourth through sixth abdominal sternites (Fig. 1, ST 4-ST 6) plastral hairs occur only laterally; near the midline they are lacking. The only structures observed in this hairless region are short, blunt microtrichia, approximately 1 μm wide at the bases and 2 μm long, which project posteriorly. They are arranged in widely-spaced groups of from two to six. Each group of microtrichia arises from the slightly raised, curved, posterior edge of a roughly semicircular region of the cuticle. The microtrichia lack sockets and lie nearly parallel to the surface of the cuticle.

More posteriorly on the fourth through sixth sternites, but not as far as the posteriormost edge, the microtrichia are more numerous per group, longer (up to 3 μm), and occur in more closely-spaced groups (Fig. 11). Each group consists of 5-15 microtrichia and these, along with the region of smooth cuticle to which they attach, form a fringed, semicircular unit. The units are arranged like shingles. On this central part of the sternite, unlike the more anterior region, hairs appear to be present between adjacent rows of microtrichia. Since only the tips of these hairs are visible, we could not determine whether they are similar to the short plastral hairs which cover the lateral and posterior regions of the fourth through sixth sternites; these regions lack microtrichia (Fig. 1, unstippled portions of ST 4-ST 6).

(4) *Fringed Setae* (Fig. 12)

Fringed setae may occur either singly or in large numbers. They arise from sockets in the cuticle and project posterolaterally. A trans-

verse section through a fringed seta near its base would appear as a nearly complete circle, with the open end facing away from the cuticle. Towards the tips the setae are wider, more flattened, and would appear as more widely open arcs in transverse section. Their outer surfaces bear longitudinal grooves corresponding to pronounced ridges on their inner surfaces. The apical portion of each of these ridges subdivides into several short projections which give the seta a fringed appearance. The sizes of the fringed setae vary considerably; on the lateral edges of the ventral paratergites their length ranges from 12 to 38 μm, and their diameter from 6 to 15 μm.

Single fringed setae occur on nearly all parts of the ventral surface, but appear to be less common on the prothorax and the medial portions of the abdominal paratergites than on other regions. Large concentrations of them occur along the lateral edges of the third through eighth ventral paratergites. On the second paratergite the leaf-like setae extend all the way to the lateral edge, and there are few fringed setae. On the most posterior segments, however, the extreme lateral portions of the paratergites bear fringed rather than leaf-like setae. They occur in largest numbers on the edges of the fifth, sixth, and seventh abdominal segments and become increasingly less numerous on each of the more anterior ones. The eighth paratergite bears fewer of them than the seventh.

In *Cryphocricos hungerfordi* a narrow strip bearing only plastral hairs separates the leaf-like and fringed setae, and the latter, which occur in a single row, are fewer and farther apart than in *C. barozzii.* The two types of setae are less clearly separated in *C. barozzii,* whose fringed setae are more numerous, closer together, and in several poorly-defined rows (Fig. 12). Their dense distribution on the lateral edges of the fifth through seventh paratergites in this species suggested, at first, that they might be hydrofuge devices. On the paratergites of *C. hungerfordi,* however, they appear to be too far apart to function in this way. Their sporadic occurrence on nearly all the exposed surfaces of the body suggests that they have some other function, probably a sensory one.

Dorsal Surface

The dorsal surface of the body was studied only briefly in one specimen of each species of *Cryphocricos.* In both specimens this surface is covered with considerably more silt and debris than the ventral one. The detritus clings to all the parts of the dorsum which are exposed to the water (Fig. 2, left side); these regions have a roughened appearance under the stereoscopic microscope.

The surfaces which are concealed by the shortened forewings, however, are relatively free of debris. Except for the third abdominal tergite (Fig. 2, T_3) these regions appear smooth under the stereoscopic microscope (Fig. 2, light stippling on right side). The smooth terga and the inner (ventral) surfaces of the forewings lack fringed setae and are covered with densely-packed hydrofuge hairs. Those on the metatergum (T III) and second abdominal tergite (T 2), which were examined in more detail, possess nodules basally, are at least 5 μm long, and have diameters similar to those of the plastral hairs on the ventral surface of the body. The hairs on the inner surface of the forewing are considerably shorter (approximately 1.5-2 μm in length) than those on the second abdominal tergite and metatergum. Basal nodules were observed on these alar hairs only in the region of the forewing which is externally visible in ventral view (Fig. 1, FW); here the hairs are longer, but since their tips appear to coalesce their height could not be estimated.

The surfaces which are exposed to the water are covered with small, wart-like, cuticular protuberances which give them a roughened texture. The raised surfaces of these protuberances, which are approximately 20-35 μm in diameter and one to two times this distance apart, lack hairs. Each "wart" bears a small central indentation containing a curious fringed papilla, possibly a sensory device. The large spaces between the protuberances were, unfortunately, covered with debris on all of the exposed abdominal tergites. The anterior third of the third abdominal tergite, however, is overlapped by the posterior edge of the forewing, which largely protects it from debris. In this region, densely-packed hairs, at least 5 μm long and 0.3 to 0.4 μm wide at the tips, cover the areas between the cuticular "warts". Similar hairs occur between the protuberances on the exposed portion of the mesothoracic tergum (Fig. 2, T II). Quite probably hydrofuge hairs are present between the protuberances on the prothoracic and fourth through seventh abdominal terga, but are hidden beneath the debris. Occasional fringed setae occur on all of the exposed dorsal surfaces of the body, and are especially numerous along the lateral edges of the abdominal terga and in the abdominal intersegmental sulci.

Discussion

Although in most areas the fringed setae appear to be too widely spaced to retain an air layer, at least two of the other three types of fine structures on the cuticular surface of *Cryphocricos* appear to be

plastral devices. The densely-packed hairs on the ventral surfaces of the thorax and abdomen strongly resemble those of *Aphelocheirus,* which has plastral respiration (Thorpe and Crisp 1947a) and differ from those of *Pelocoris,* which has "air-bubble" respiration (Parsons 1974). The microtrichia in the central portions of the fourth through sixth abdominal sternites have a shingle-like arrangement which strongly resembles that of the plastral devices on the sternites of *Torridincola* (Coleoptera, Hinton 1969b); these microtrichia, along with the hairs between them, probably also retain a thin layer of air.

The function of the leaf-like setae on the paratergites is more problemmatic. They may serve merely to protect the underlying plastral hairs from becoming too clogged with debris to allow the adherent air layer to carry on gas exchange with the water. Although they may, indeed, do this, it is unlikely that it is their sole function, since they are absent in other regions with plastral hairs. In *Aphelocheirus,* which is also covered with debris, leaf-like setae occur only on the second abdominal sense organs, but the experiments of Thorpe and Crisp (1947a, 1947b) have shown that the insect is able to maintain efficient plastral respiration.

The presence of large amounts of air among the elongated leaf-like setae on the sense organs of *Cryphocricos* suggests that the shorter ones on the rest of the paratergites are similarly capable of retaining air, although in smaller and less visible amounts. They may well act in conjunction with the underlying plastral hairs, in much the same way that long and short hydrofuge hairs hold a "macroplastron" external to a "microplastron" in some aquatic Coleoptera such as *Hydrophilus piceus* (Thorpe and Crisp 1949). Like the long hairs which retain the "macroplastron" in the latter, the leaf-like setae may, under increased hydrostatic pressure, help to protect the thin layer of air, which is trapped in the underlying short hairs, against water entry. When the insect dives to regions of increased pressure the posterolateral slope of the setae may increase, so that the setae become pressed together and form a barrier against water penetration. Their presence only on the paratergites, and their absence in other regions, may be connected with the need to protect the second through eighth abdominal spiracles, which lie on the surfaces of the paratergites, against flooding. The three more anterior pairs of spiracles (mesothoracic, metathoracic, and first abdominal) are concealed within invaginations of the exoskeleton and are thus more protected than the posterior ones against the entry of water.

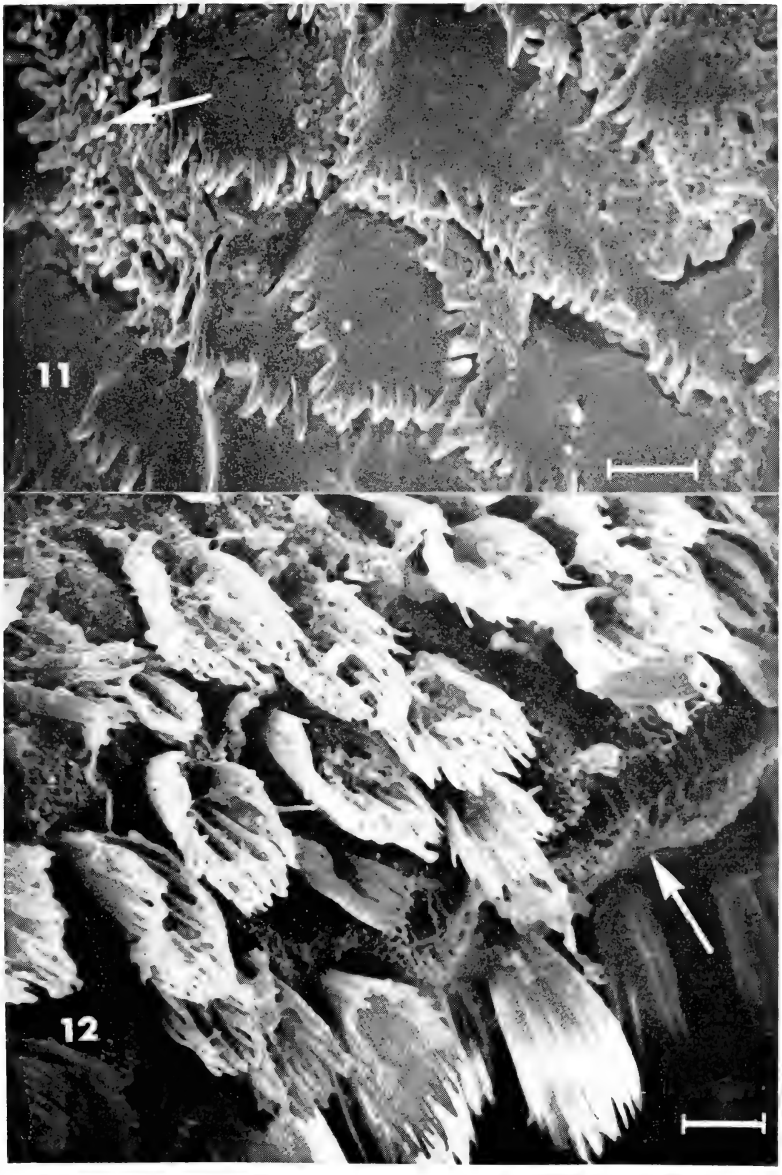
Thorpe and Crisp (1947c) have described how the elongated setae on the abdominal sense organs of *Aphelocheirus* become compressed under increased pressure, stimulating shorter sensory hairs which are interspersed among them, and thus warning the insect against diving to dangerous depths. The elongated leaf-like setae on the six pairs of abdominal sense organs of *Cryphocricos* probably have a similar function, and the shorter leaf-like setae on the rest of each paratergite may have evolved from these longer ones.

The efficiency of the plastron in *Cryphocricos* cannot be determined without experiments similar to those which Thorpe and Crisp (1947a, 1947b) performed on *Aphelocheirus*. Nearly all of the ventral surface of *Cryphocricos*, and at least a part of the exposed dorsal surface, bear apparent hydrofuge devices. If these devices do, indeed, retain a thin, permanent, plastral air layer, a considerable surface area of air is exposed to the water and is capable of gas exchange with the latter. Dissolved oxygen could pass directly to the mesothoracic, metathoracic, and second through eighth abdominal spiracles, all of which face portions of the ventral plastron. Although the dorsal subalar space is not exposed to the water, it communicates with the ventral air layer by means of the narrow gap between the ventrally exposed portion of the forewing (Fig. 1, FW) and the ventrolateral edge of the body. The hydrofuge hairs lining this gap would permit a small amount of oxygen to pass from the ventral plastron to the first abdominal spiracle, which faces the subalar space (Parsons 1974). The extent to which the spiracles, especially the first abdominal ones, are capable of inhalation is not known, however, and will require experimentation and further fine-structural studies.

There is a strong possibility that well-developed plastral respiration has evolved in other Naucoridae, as Hinton (1969a) claims. Further investigation will probably reveal it not only in other members of this family but quite possibly in other families of aquatic Heteroptera as well.

Fig. 11. *C. barozzii;* shingle-like arrangement of several groups of microtrichia on median portion of fourth abdominal sternite, approximately midway between its anterior (towards top) and posterior (towards bottom) boundaries. Arrow indicates where tips of hairs, mostly concealed by debris, appear to be interspersed among groups of microtrichia. Scale line = 5 μm.

Fig. 12. *C. barozzii;* large numbers of fringed setae on lateral edge of sixth ventral abdominal paratergite, left side of body. Arrow indicates edge of body. Scale line = 10 μm.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Acknowledgments

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Summary

The scanning electron microscope shows that in *Cryphocricos barozzii* and *C. hungerfordi* most of the ventral surface of the body and at least a part of the dorsal surface are covered with fine structures which appear to be hydrofuge devices. Both surfaces bear short, fine hairs which are very similar to those of *Aphelocheirus aestivalis,* the only aquatic heteropteran in which plastral respiration has thus far been demonstrated. These hairs are much smaller and more densely-packed than those of *Pelocoris femoratus,* which carries a large air bubble and relies upon atmospheric oxygen. On the ventral abdominal paratergites of *Cryphocricos* the plastral hairs are covered by curious, leaf-like, ridged setae which overlap each other and perhaps retain a "macroplastron". Very elongated leaf-like setae occur on the six pairs of abdominal pressure receptors of *Cryphocricos. Aphelocheirus* possesses leaf-like setae only on its single pairs of abdominal sense organs. The fourth through sixth abdominal sternites of *Cryphocricos* bear groups of microtrichia with a shingle-like arrangement; they resemble the plastral devices of some aquatic Coleoptera. These fine structural observations strongly suggest that *Cryphocricos* has plastral respiration and utilizes dissolved rather than atmospheric oxygen.

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HOME RANGES OF MALE *CERCERIS SIMPLEX MACROSTICTA* (HYMENOPTERA, SPHECIDAE)*

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Although it is well known that many sphecid males visit flowers and shrubs and attempt to mate with females found there (e.g. Peckham, Kurczewski, & Peckham, 1973), many unanswered questions about this general pattern of male behavior remain. For example, do flower-visiting males move randomly from area to area or do they remain in one location for substantial periods of time? If they show an attachment to a particular site, do they defend the area or do they share it with other males?

We addressed these questions for one species by studying males of *Cerceris simplex macrosticta* Viereck and Cockerell at two separate sites along State Line Rd., ½ km west of Rodeo, New Mexico. Study area 1 consisted of a strip of roadside ditch, 75 m × 2 m, covered with a dense stand of flowering milkweeds (*Asclepias subverticillata*). Two mesquites and a sprawling multiflora rosebush were the only large plants at this location. Study site 2, located several hundred meters from study site 1, was an area roughly 25 m × 10 m in an uncultivated pear orchard overrun with clumps of Russian thistle (*Salsola kali*) and dotted with scattered flowering weeds. From 23-27 July 1974 sixteen males were captured in these two areas and marked on the dorsum of the thorax with acrylic paints, each individual receiving a distinctive color or color combination. One or more censuses were made at the two sites on all days from 23 July to 8 August with the exception of 2, 4, and 7 August.

Results

Home ranges of *C. simplex*

Nine of the marked males were seen again at or near the location where they had been originally captured and seven of the sixteen males were followed for a week or more (Table 1). The failure to relocate six marked individuals could be attributed to a variety of factors including mortality and the passage of transient males from the study areas.

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Table 1. Site attachment of male *C. simplex*. A total of sixteen individuals marked 23-27 July.

Days At Site										
1	2	3	4	5	6	7	8	9	10	11
Number of Wasps										
6	1	1				1	2	1	2	2

The resident males were repeatedly observed pursuing regular circuits between 0839-1230 hrs. and rarely as late as 1400 M.S.T. Four carefully studied individuals possessed routes ranging from 7.0-18.5 m in length and from 2-3 m in width (Fig. 1). However, marked wasps also made occasional forays up to six m from their customary route. Males in the roadside ditch cruised in a fairly rapid and erratic flight going down one side of the ditch skimming over flowering *Asclepias,* and then back up the other. Orchard males flew from one clump of *Salsola* to another sailing around and over them, sometimes visiting flowering weeds along the route (Fig. 1).

Wasp "yellow" had the smallest circuit of the males we studied and required a mean of 32 sec to complete one flight about its home range ($N = 9$; range, 22-68 sec; 28 July, 0820-1115). Most of a male's time was spent in flight, although the wasps regularly alighted on perches in their cruising area (Fig. 2). For example, "white" landed on one branch of a rose bush 16 times in 35 minutes (23 July) remained perched an average of 6:5 sec (range, 1-19 sec). Several males had a primary perch to which they commonly returned as well as several secondary perches that were used less frequently.

Males pursued any medium-sized flying insect including a wide variety of wasps, beeflies, and brilliant black and red hemipterans as well as male and female conspecifics. Males made physical contact *only* with conspecific females. The indiscriminate nature of the pursuit flight and the absence of grappling or contact between males leads us to believe that male *C. simplex* lack behavior designed to defend a territory. The great overlap in routes travelled by different males (at least four males regularly entered "blue's" circuit and easily that many were present in "white's" area) further suggests that males of this species occupy home ranges and not territories.

Attempted matings

Despite many hours of observation, attempted copulations were seen only three times (at 0915, 0925, 1030), all in the orchard. In one case a female cruised slowly through a *Salsola* clump occa-

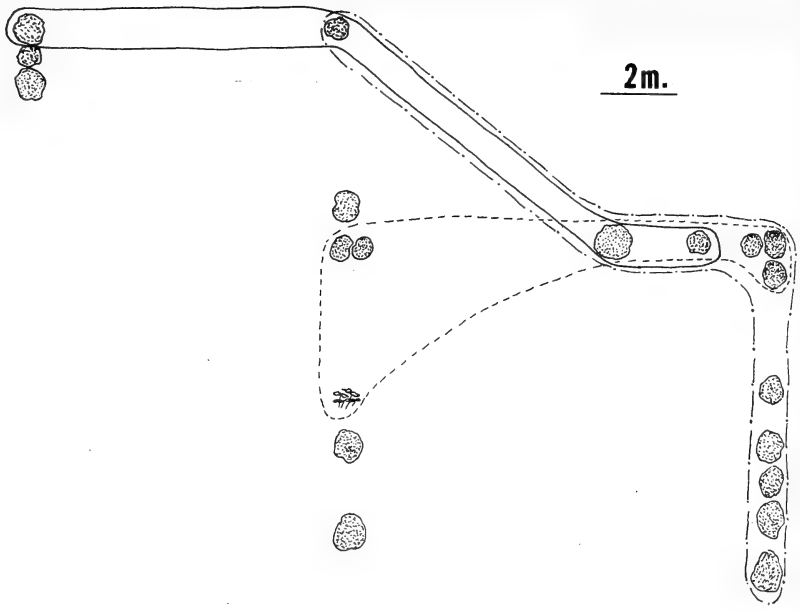

Fig. 1. The overlapping home ranges of three males at the orchard study area. "Blue's" home range is outlined with a dashed line; "red's" home range is outlined with a dot-dashed line; "white-dot's" home range is outlined with a solid line. The circular stippled areas represent prominent *Salsola* bushes. One large flowering weed is shown schematically in the lower left hand corner of "blue's" home range.

sionally alighting and walking up stems apparently searching for prey, the tenebrionid beetle *Metapoloba pruinosa* (Alcock, 1974), which were sometimes seen in this plant. As she flew slowly past a perched male he flew up and cruised behind her. The female alighted and the male quickly dropped onto her back facing in the same direction as his potential mate. While stroking her antennae with his the male held the female's wings out at right angles to her body by sandwiching each wing between his fore- and midlegs, presumably making escape more difficult for the female. His hindlegs grasped the female's abdomen. After several minutes of unsuccessful attempts to copulate, the male released his partner and both flew away. The other two attempted matings also followed this general pattern. One took place in a *Salsola* plant, the other on a flower head of a weed. The related wasp *C. frontata* also mates at flowers, initially adopting the position used by *C. simplex* (pers. obs.) with the male dismounting after coupling is achieved (Scullen, 1965).

Sleeping sites

In the late afternoon, especially before impending storms, males were seen flying slowly along the large rose bush. The wasps eventually alighted and walked under groups of tightly packed leaves and, in one case, into a tube formed by a rolled leaf, evidently in search of a sheltered sleeping site. One male ("red") that had been marked on the morning of 27 July at a spot 50 m to the south of the rose bush was found by this plant at 1610 seeking a resting place before a thunderstorm. The next morning it had returned to the area where it had been marked indicating that some males may fly modest distances from their home range in order to exploit a sleeping site.

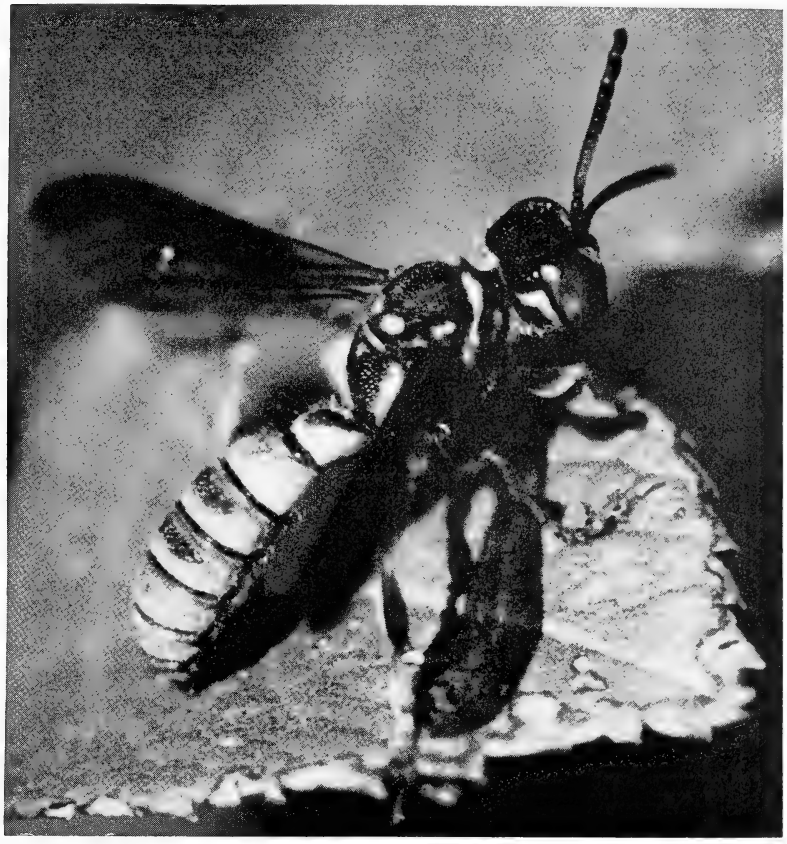

Fig. 2. A male *Cerceris simplex* perched on a rose leaf and resting between cruising flights about its home range.

Discussion

To the best of our knowledge *C. simplex* provides the only documented example of a wasp species whose males occupy fairly extensive home ranges in areas away from an aggregation of nesting females. Doubtless this only reflects the lack of research of male wasps and it is probable that home ranges embracing patches of flowers are a common phenomenon in male sphecids.

The spacing system of male *C. simplex* does, however, differ from that of various close relatives, among them several species of *Eucerceris* as well as *Philanthus* and *Clypeadon* (Alcock, 1975 and in prep.). Males of these related species form relatively dense aggregations with each individual applying an attractant pheromone from abdominal glands to a perch and vigorously repelling all intruders from an area roughly ½-1 m in radius around the perch. Whether all the members of one genus share the same basic mating strategy is unknown and will require much further study, although the very limited current information hints that this may be the case (Alcock, in prep.).

Despite the differences between *C. simplex* and other philanthinine wasps there are some similarities as well. In all cases males occupy a perch to which they return after bouts of flying around. All pursue a remarkably wide range of flying insects evidently in an effort to determine the species and sex of the passerby or intruder. The key variable between different species is the area inspected by an individual. Those males that use a perch as a calling post defend it and a small area around it while *C. simplex,* which does not appear to employ an attractant pheromone, covers a much larger area (up to at least 40 m^2), so large as to be essentially indefensible. Attempts to drive all other males from a strip of roadside ditch 15 m × 2 m would require an extraordinary investment in aggressive territorial patrolling. Instead, *C. simplex* males make no special effort to locate and repel conspecific males. Time and energy are devoted to repeated investigation of a large area in a location likely to attract females, one which is rich in nectar-producing flowers or beetle-producing bushes. Having found a potentially good area, males remain there becoming familiar with its prime spots. Presumably this is a superior strategy than one that would take a male on a random journey through the countryside in search of a mate. Because naturally occurring attractants (e.g. flowers) that draw in females tend to be patchily distributed, one would predict that males of other species that use such attractants to focus their search for females will

also possess home ranges. Additional comparative data based on studies of marked populations of males are required to test this prediction.

Acknowledgments

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ADDITIONAL NOTES ON *STEPHANITIS TAKEYAI* IN NEW ENGLAND (HETEROPTERA: TINGIDAE)

By Norman S. Bailey

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In 1950 I reported this Asiatic lace bug as a serious pest of *Pieris japonica* (Thunberg) Don in Greenwich, Connecticut, and the surrounding area. Since 1956 I have been teaching at Bradford College, in northeastern Massachusetts. Although there are several specimens of *Pieris* on the rather nicely landscaped campus and in the planting around a college house I lived in for many years, I saw no evidence of lace bugs until the fall of 1973. On that occasion I searched the plants showing considerable injury but failed to find any tingids.

On September 9, 1974, however, I noted that the same plants showed typical signs of severe feeding injury and found numerous nymphs and adults of *Stephanitis takeyai* on the undersides of the leaves of two Japanese Andromedas.[1] These plants grow in a mixed shrub planting along the north foundation of our main lecture hall. In the same foundation planting are such other evergreen ericaceous shrubs as *Pieris floribunda* Bentham & Hooker, *Rhododendron carolinianum* Rehder, *Kalmia latifolia* L., *Leucothoë catesbaei* Gray, and a few deciduous azaleas. With the exception of an azalea, whose branches intermingle with one of the infested *Pieris japonica,* there was no evidence of lace bug feeding nor did I find any tingids on the other ericaceous plants. This particular azalea, which may be *R. calendulaceum* Torrey, does show lace bug injury and specimens were collected from it. Many of its leaves had also been almost skeletonized in a way that suggested Japanese beetle damage.

A few days later I found another heavily infested *Pieris japonica* in a planting near a small building towards the south end of the campus. This suggested checking further. On October 1st, two more plants were found on the front campus with tingids present in some

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[1]The original name of this species, *globulifera* Matsumura, turns out to be a junior homonym, and it was renamed *takeyai* by Drake and Maa, 1955. See also Drake and Ruhoff, 1965.

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numbers. One grows on the north corner of our auditorium and the other on the west side of the same building. The latter grows beside a hybrid *Rhododendron* that also showed considerable leaf discoloration, especially on leaves of the previous year. This year's growth was only thinly specked with fine whitish dots on the upper surface and no lace bugs were located on either the older or the newer foliage of this plant.

On October 3rd I extended the search and inspected *Pieris japonica* specimens in the front foundation plantings of five college owned houses situated on the opposite sides of the two streets that parallel the east and the west sides of the main campus. A sixth house is on a road beyond the tennis courts at the southern edge of the college property and about a half a mile from the front of the campus where specimens were first found. All of the plants observed showed some evidence of injury and several were heavily infested. In spite of light frosts on at least two nights recently, temperatures below 40°F for another two nights, and only in the low fifties during the two consecutive days, adults (some teneral) and nymphs of *Stephanitis* were numerous and active on some of these *Pieris* on October 3rd and 4th.

On the 4th a collection was taken from a *Pieris japonica* by the northeast entrance to the campus. This plant had numerous nymphs and some adults on the leaves. At least four nymphal instars are represented in this one late season collection. The smallest nymph, without apparent spines, was 0.7 mm. long. Others measured 1.2 mm., 1.8 mm. and 2.4 mm. in length and these all had prominent spines on the dorsal side of head, thorax, and abdomen Three adults found with them measured from 3.9 to 4.2 mm.

Although many leaves were examined (several with the aid of a stereoscopic microscope), no evidence of eggs was discovered. Therefore, the late occurrence of early nymphal instars and of teneral adults strongly indicates that *S. takeyai* may over-winter in these stages, contrary to my earlier suggestion (1951). Obviously this point needs clarification.[2]

On October 26th, specimens of *Pieris japonica* showing characteristic discoloration were seen in Haverhill at least two miles from the

[2]While this paper was in press, I received a copy of Dr. Dennis Dunbar's recent (1974) article on this tingid, in which mention is made of the general occurrence of *takeyai* in southern New England, without giving specific localities in Massachusetts. The same paper provides a full account of the life history in Connecticut and indicates the species lays eggs that overwinter in the *Pieris* leaves there.

campus and north of the Merrimac River. The campus is in a residential area south of the river. Obviously this lace bug is now well established locally. The leaves of *Pieris japonica,* much discolored and damaged by the heavy feeding of *Stephanitis,* tend to drop prematurely. Consequently, gardeners and nurserymen should be concerned with the spread of this lace bug from southwestern Connecticut into northeastern Massachusetts.

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A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room B-455, Biological Laboratories, Divinity Ave., Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

The illustration on the front cover of this issue is of Samuel Hubbard Scudder of Cambridge, who, along with Professor Hagen, provided the initiative for the founding of the Cambridge Entomological Club and a Psyche in 1874. It is taken from a photograph in the archives of the Museum of Comparative Zoology.

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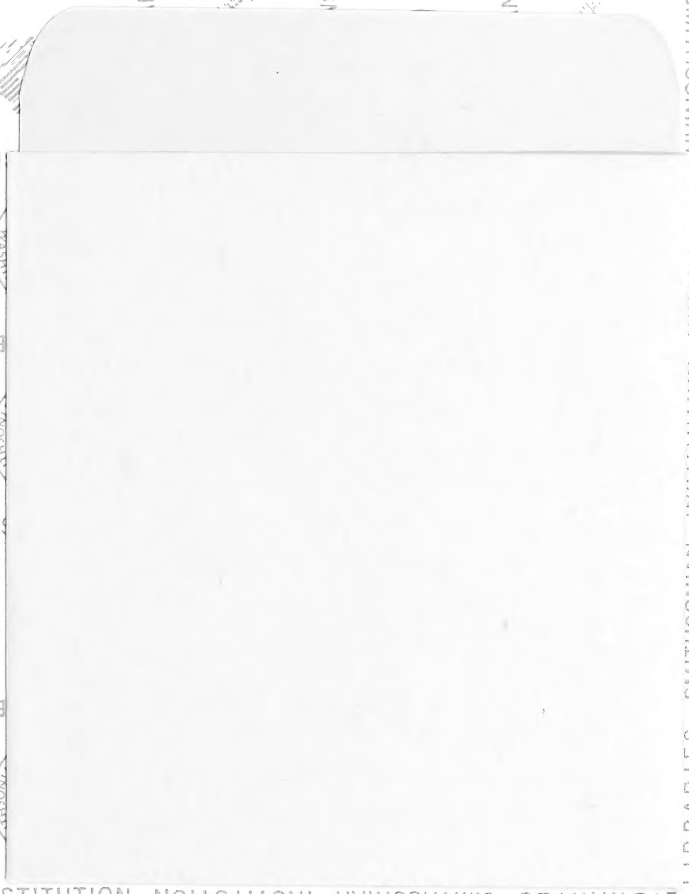

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